

Ultrasonic treatment decreases *Lyophyllum decastes* fruiting body browning and affects energy metabolism

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ABSTRACT

Lyophyllum decastes is a common mushroom that is prone to browning during prolonged storage. In this study, the effects of ultrasonic treatment on metabolic gene expression, enzyme activity, and metabolic compounds related to *L. decastes* browning were investigated. Treatment of the fruiting body at 35 kHz and 300 W for 10 min reduced the browning index of *L. decastes* by 21.0 % and increased the L* value by 11.1 %. Ultrasonic treatment of the fruiting body resulted in higher levels of total phenols, flavonoids, and 9 kinds of amino acid with catalase (CAT) and peroxidase (POD) activities maintained at high levels. Higher cytochrome c oxidase (CCO), succinate dehydrogenase (SDH), phosphofructokinase (PFK), and pyruvate kinase (PK) activities may be ascribed to increased antioxidant capacity. Moreover, ultrasonication retained higher adenosine triphosphate (ATP) concentrations with an increased energy charge, while there were lower levels of adenosine diphosphate (ADP) and reduced and oxidized nicotinamide adenine dinucleotide (NADH and NAD⁺), respectively. Meanwhile, lower lignin contents were observed, along with retarded polyphenol oxidase (PPO) and lipoxygenase (LOX) activities. Lower PPO activity reduced the fruiting body enzymatic browning rate through decreased expression of *LdPpo1*, *LdPpo2*, and *LdPpo3* during storage at 4 °C for 16 days. This activity may be used to determine the effectiveness of ultrasonication.

1. Introduction

Lyophyllum decastes is a popular edible mushroom because of its high nutrient content, including polysaccharide, protein, and essential amino acids [1]. It has a broad market due to its delicious taste and crisp texture [2]. However, fresh mushrooms are considered highly perishable due to browning, fibrosis, and quality deterioration, which reduces commodity acceptance and storage quality after postharvest [3].

Enzymatic browning is one of the important factors affecting quality deterioration of harvested horticultural products [4]. The oxidase activity and phenol content related to fruit and vegetable growth and mature aging regulates the enzymatic browning rate [5]. Ultrasonic treatment significantly decreased polyphenol oxidase (PPO) activity in

fresh *Volvariella volvacea* while maintaining firmness and storage quality [6]. Melatonin application at 0.1 mM retarded pulp browning of fresh-cut pear, with significantly reduced PPO activity and browning index (BI), whilst maintain high total phenol content and increase the antioxidant capacity [7]. Decreased PPO activity improved the storage quality of lettuce, potato, and fresh-cut taro [8–10].

Energy metabolism related to storage tolerance and physiological metabolic activities affected quality deterioration of postharvest fruit and vegetables [11]. Litchi storage quality is related to energy levels and H⁺/Ca²⁺/Mg²⁺-ATPase activities, fresh litchi treated with hydrogen peroxide (H₂O₂) decreased the energy level and deteriorated the storage quality [12]. Meanwhile, litchi fruit treated with melatonin increases the activity of key respiratory enzymes such as succinate dehydrogenase

Abbreviations: CAT, Catalase; POD, Peroxidase; CCO, cytochrome c oxidase; SDH, succinate dehydrogenase; PFK, phosphofructokinase; ATP, adenosine triphosphate; ADP, adenosine diphosphate; AMP, adenosine monophosphate; PPO, polyphenol oxidase; LOX, lipoxygenase; BI, browning index; PK, pyruvate kinase; GOGAT, glutamine oxoglutarate aminotransferase; GDH, glutamate dehydrogenase; NADH, nicotinamide adenine dinucleotide1; NAD⁺, nicotinamide adenine dinucleotide; GAPDH, glyceraldehyde 3-phosphate dehydrogenase.

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Table 1
The sensory evaluation criteria.

Score	Color	Smell	Texture	Condensate inside the crisper	Consumer acceptance
5	grey-brown brightness	typical fresh mushroom aroma	firmness	slightly condensed water beads	satisfaction
4	brown brightness	moderate fresh mushroom aroma	moderate firmness	partly condensed water beads	moderate satisfaction
3	brown moderate brightness	moderate mushroom aroma	moderate	clusters of condensed water beads	acceptance
2	mid-brown slight brightness	non-mushroom aroma	slightly soften	string of condensed water beads	moderate acceptance
1	mid-brown non brightness	slight odor	soften	large area of condensed water beads	lower acceptance

Table 2
All primers used in this study.

Primers	Sequence	Note
LdPpo1-F	5'- GAACTACACCCTCCACCTG -3'	for qRT-PCR
LdPpo1-R	5'- CGTGTCATATCGCTGTAGTT -3'	for qRT-PCR
LdPpo2-F	5'- CTAGTCCTGGAGGTTGTTG -3'	for qRT-PCR
LdPpo2-R	5'- CAGCATATCCGATCGAGGTTG -3'	for qRT-PCR
LdPpo3-F	5'- ACGTACGATCTTCGCAATGT -3'	for qRT-PCR
LdPpo3-R	5'- CACAGATAACCGCCTTGAT -3'	for qRT-PCR
LdGAPDH-F	5'- TCAATGCGACGAGTAAAGAGAGG -3'	for qRT-PCR
LdGAPDH-R	5'- CATAGGTCCACATCTACATTTCG -3'	for qRT-PCR

(SDH) and cytochrome *c* oxidase (CCO), maintains high energy levels, lowers the BI of fruit peel, and reduces the litchi fruit aging rate during cold storage [13]. Therefore, energy metabolism plays an important role in browning of postharvest horticultural products. At present, many studies focus on the active substances of mushrooms (*L. decastes*) and there are few reports on enzymatic browning and energy metabolism to improve storage quality.

Ultrasonic (US) treatment can retard enzyme activities related to enzymatic browning, retain the surface color to delay shelf-life and

maintain higher commodity value, and increase consumer acceptance of postharvest horticultural products [14]. US treatment of *V. voluacea* at 49 kHz increased its firmness, postponed weight loss and the cryogenic autolysis rate, and increased the storage quality [15]. There are few studies analyzing the effect of US treatment on enzymatic browning of edible mushrooms combined with energy metabolism.

In this study, the effect of US treatment (35 kHz, 300 W and 10 min) on fruiting body browning, enzymatic activity, energy level, and *LdPpo* gene expression pattern in *L. decastes* was explored during low temperature postharvest storage. Our findings may provide a strategy to decrease the enzymatic browning rate and improve the storage quality of *L. decastes*.

2. Materials and methods

2.1. Mushroom treatment and storage

Fresh mushrooms (*L. decastes*; 8–9 maturity) were collected from Zhen Jun Zi Biotechnology Co., Ltd. (Fujian, China) and selected for uniform size, a complete cap, and excluding any mechanical damage and cracked stalks. They were sent to the laboratory of College of Food Science, Fujian Agriculture and Forestry University for pretreatment on the same day. The tested fruit were precooled for 30 min at 4 °C, then randomly divided into 2 groups: CK (control) and US.

The US group involved placing fruiting bodies (250 ± 10 g) into slip lock sealed plastic bags of 23 × 15 × 7 cm, thickness 0.06 mm, polyethylene (PE) texture, Shanghai shiling culture communication Co., Ltd. (Shanghai, China), and placed in ultrasonic cleaner (SK8210LHC, China), treated with 35 kHz, 300 W, water bath (4 °C) for 10 min. The bag was removed from the instrument, and the mushrooms were replaced into a fresh bag with plastic tray (17.5 × 10 × 4.5 cm), Zhen Jun Zi Biotechnology Co., Ltd. (Fujian, China) for storage at 4 ± 0.5 °C for 16 days. The samples in the CK group were stored at 4 ± 0.5 °C for 10 min, then separated into a slip lock sealed plastic bags (250 ± 10 g per bag) and stored under the same conditions as the US group. The packed process at atmospheric pressure condition, every bag had no swelling phenomenon.

Five mushrooms per replicate of each treatment were immediately sampled (day 0), then taken on days 4, 8, 12, and 16 of storage at 4 °C. Samples were placed into liquid nitrogen, then quickly stored at −80 °C for gene expression and biochemical analysis.

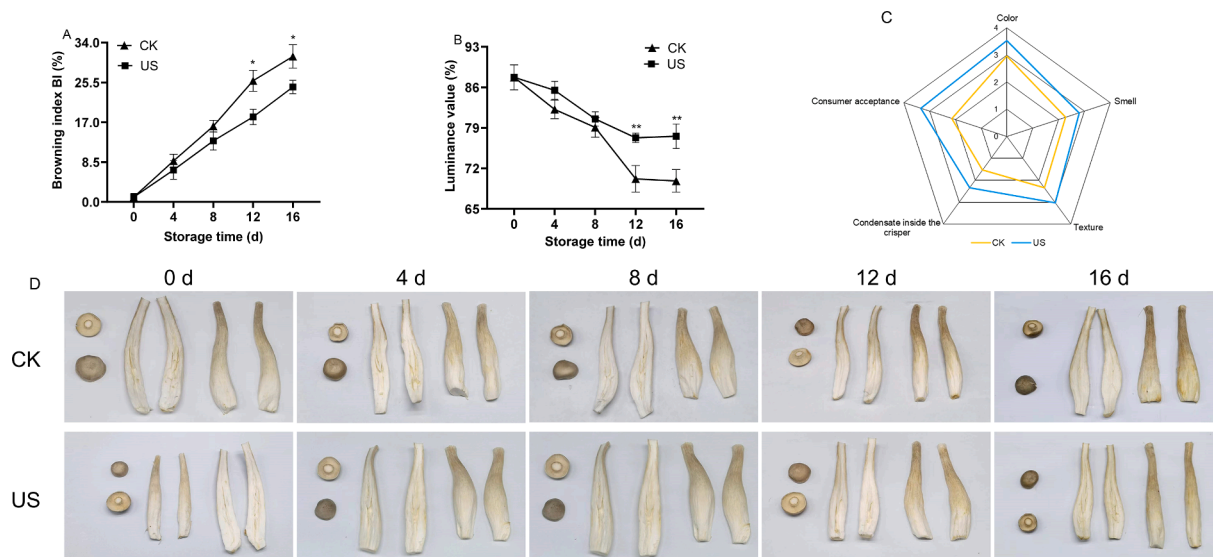


Fig. 1. Effect of US treatment on the Browning index (A), L^* value (B), sensory score (C): on day 16 and sensory quality (D) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

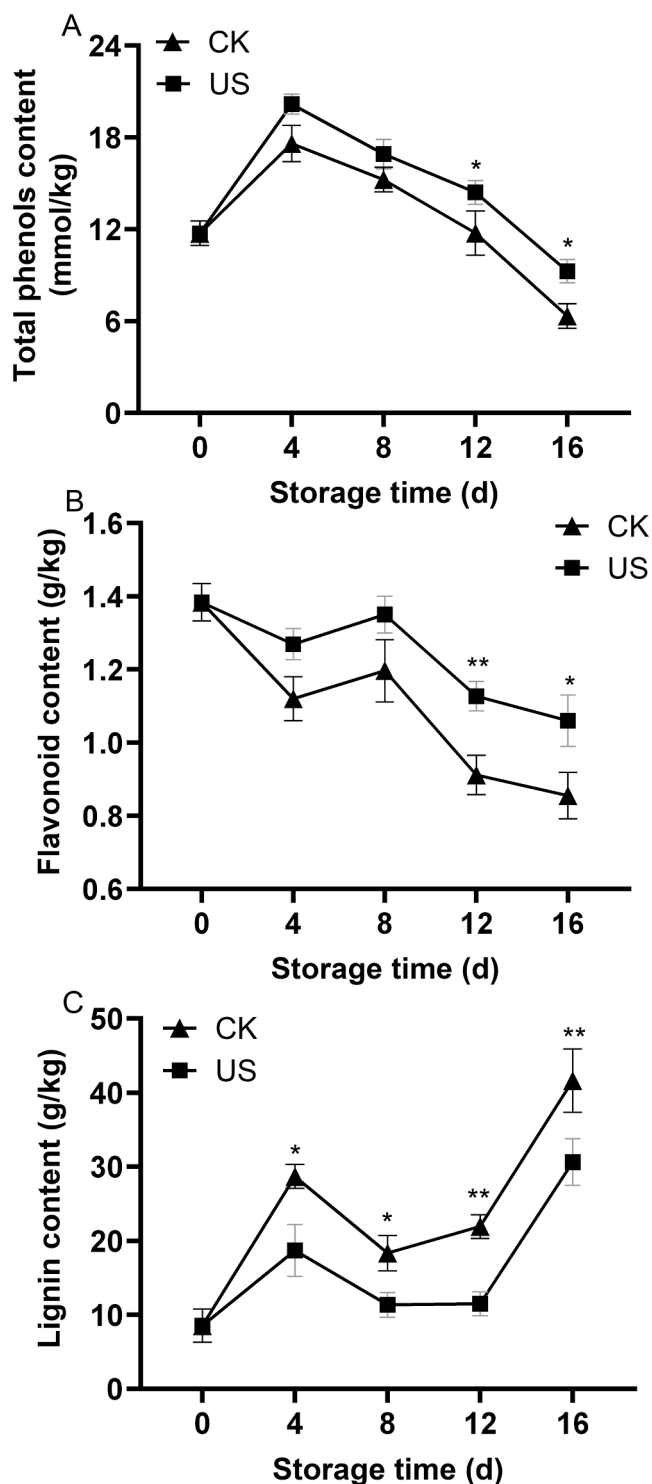


Fig. 2. Effect of US treatment on the content of Total phenol (A), Flavonoid (B) and Lignin (C) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences ($p < 0.05$, $** p < 0.01$).

2.2. Browning index (BI) and L^* value measurement

The surface color (Browning degree) of the middle of the fruiting body was evaluated every 4 days during storage at 4 °C with a DCI-60-C automatic colorimeter (Beijing Chentech Instrument Technology Co., Ltd. China) to analyze the L^* (light / dark), a^* (red / green), and b^* (yellow / blue) values. The BI was determined using the method of Hsieh

et al. [16] according to Eq. (1).

$$BI = [100(X - 0.31)]/0.172 \quad (1)$$

where $X = (a^* + 1.75 L^*) / (5.645 L^* + a^* - 3.012b^*)$.

2.3. Sensory evaluation

Sensory evaluation was performed by a group of 10 specialized persons according to Yang et al. [17], and the indicators was modified. The mushrooms quality was evaluated on a five-point scale, and based on the color, smell, texture, condensate inside the crisper and consumer acceptance, the sensory evaluation criteria are shown in Table 1.

2.4. Free amino acid content

Individual free amino acids were determined according to Zhao et al. [18] with slight modifications. Briefly, 0.5 g freeze-dried samples were added to 5 mL of distilled water, homogenized, then treated with an ultrasound frequency of 35 kHz at 500 W for 2 h at 40 °C. Samples were centrifuged at $12,000 \times g$ for 10 min at room temperature. Four hundred microliters of the supernatant collected, followed by the addition of 200 μ L 0.1 mmol/L phenyl isothiocyanate in 1.0 mmol/L triethylamine and incubated for 30 min at room temperature. Eight hundred μ L of *N*-hexane was added, followed by centrifugation at $10,000 \times g$ for 5 min. This step was repeated, the supernatants were discarded, filtered through a 0.45 μ m filter, and then analyzed by high performance liquid chromatography (HPLC) using a Hitachi LC-20 instrument (Tokyo, Japan).

2.5. ATP, ADP, and AMP levels and energy charge

Adenosine triphosphate (ATP), adenosine diphosphate (ADP), and adenosine monophosphate (AMP) levels were determined according to the method of Wu et al. [19] with slight modifications. Briefly, 0.5 g freeze-dried samples were added to 1.2 mL of distilled water, homogenized, boiled for 5 min, and centrifuged at $8,000 \times g$ for 10 min at room temperature. The supernatants were collected, with 1 mL filtered through a 0.45 μ m filter and analyzed by HPLC. The energy charge was calculated according to Eq (2):

$$EC = (ATP + 1/2ADP)/(ATP + ADP + AMP) \quad (2)$$

2.6. Enzyme activities and contents of substance

PPO (A136-6-6, OD = 420 nm), catalase (CAT, A007-1-1, OD = 405 nm), peroxidase (POD, A-84-3-1, OD = 420 nm), CCO (A090-1-1, OD = 550 nm), SDH (A022-1-1, OD = 600 nm), phosphofructokinase (PFK, A129-1-1, OD = 340 nm), reduced nicotinamide adenine dinucleotide (NADH, A114-1-1, OD = 570 nm), nicotinamide adenine dinucleotide (NAD^+ , A114-1-1, OD = 570 nm), flavonoid (A142-1-1, OD = 502 nm), total phenols (TP, A143-101, OD = 760 nm), were examined according to the enzyme kit instructions (Nanjing Jiancheng Bioengineering Institute, Nanjing, China).

Pyruvate kinase (PK, BC0540, OD = 340 nm), lipoxygenase (LOX, BC0320, OD = 234 nm), glutamine oxoglutarate aminotransferase (GOGAT, BC0070, OD = 340 nm), and glutamate dehydrogenase (GDH, BC1460, OD = 340 nm), total sugar (BC2710, OD = 540 nm), glucose (BC2500, OD = 505 nm), fructose (BC2450, OD = 480 nm), and lignin (BC4200, OD = 280 nm) were examined according to the enzyme kit instructions (Solarbio Science & Technology Co., Ltd., Beijing, China). The test method according to the substance kit instructions, shown in supplementary Table S1.

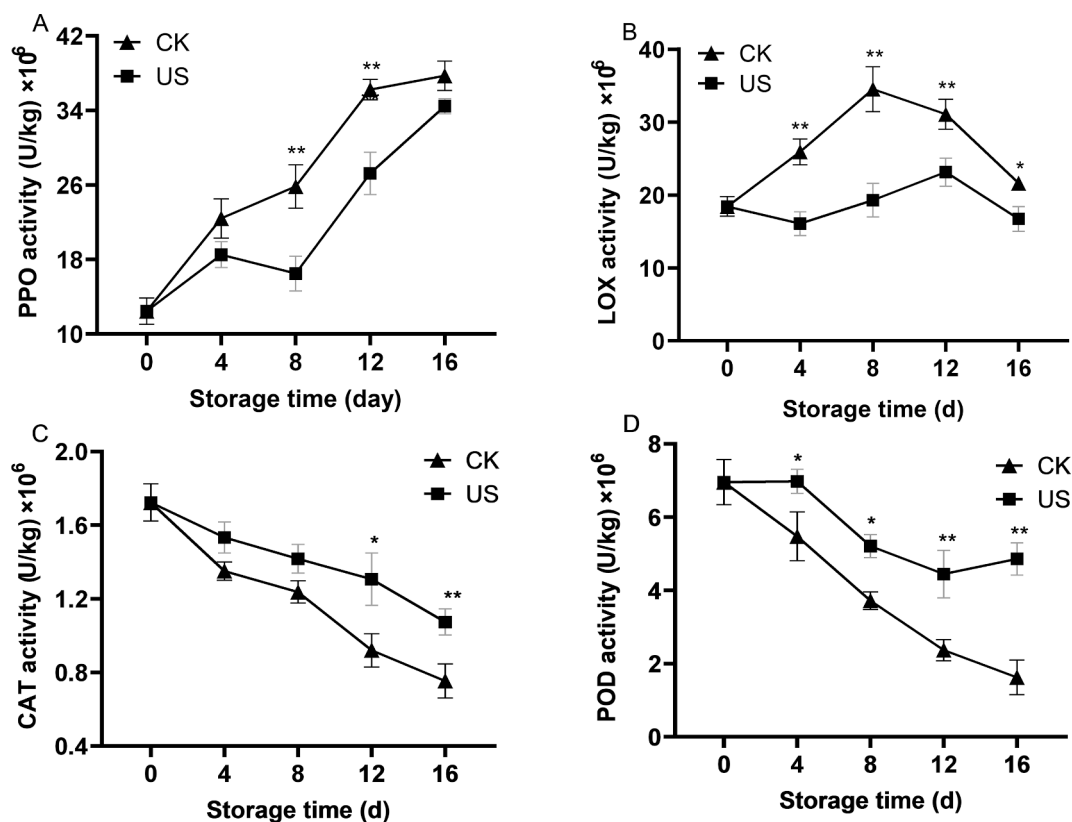


Fig. 3. Effect of US treatment on the activities of PPO (A), LOX (B), CAT (C) and POD (D) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

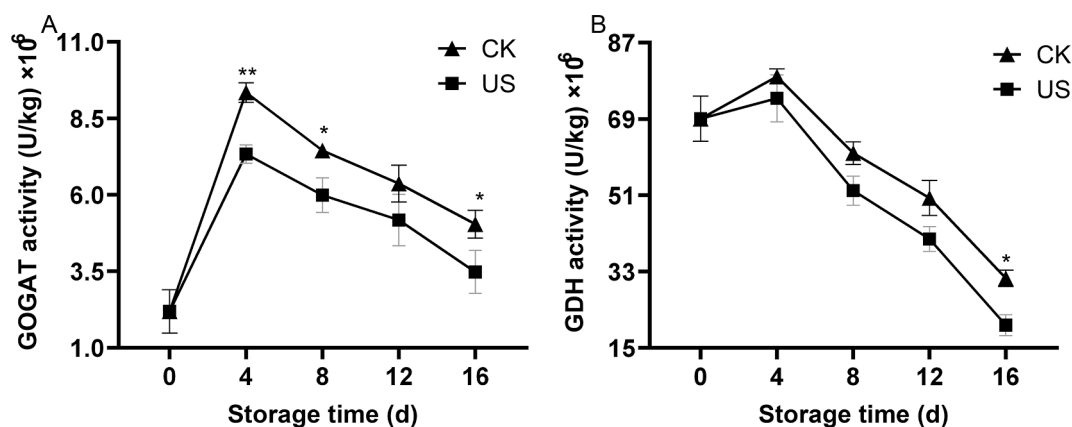


Fig. 4. Effect of US treatment on the activities of GOGAT (A) and GDH (B) of *Lyophyllum decastes* during storage during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

2.7. RNA extraction and quantitative real time polymerase chain reaction (qRT-PCR)

Total RNA was extracted according to the standard instructions stated in the E.Z.N.A. Plant RNA kit (Omega Bio-Tek, USA). cDNA synthesis was performed using the TransScript All-in-One First-Strand cDNA Synthesis SuperMix for qPCR kit (Transgen, China). The glyceraldehyde 3-phosphate dehydrogenase (GAPDH) was used as a house-keeping gene. The relative expression level was calculated following the comparative threshold cycle (Ct) value method. The changes in target gene cDNA of qRT-PCR products were normalized by GAPDH expression. The relative gene expression levels were determined according to the $2^{-\Delta\Delta Ct}$ method [20]. Primers for qRT-PCR were designed using exon

regions (Table 2).

2.8. Statistical analysis

All the indicators of each group (CK and US) were examined using three replicates. Each result in the figures represents the mean \pm standard deviation (SD). Student's *t* test was used to analyze the significance between two samples: *, $p < 0.05$; **, $p < 0.01$. Pearson's correlation analysis was used to analyze the correlation among the results.

Table 3Effect of US treatment on the contents of 11 free amino acid of *Lyophyllum decastes* during 16 days of storage at 4 °C.

Treatment	Storage time (d)				
	0	4	8	12	16
Trp (mg/kg)					
CK	394.8 ± 5.47	414.2 ± 7.33	244.2 ± 7.30	148.6 ± 6.06	117.4 ± 7.99
US	394.8 ± 5.47	475.7 ± 4.70**	393.3 ± 4.83**	244.2 ± 4.01**	161.6 ± 7.28**
Phe (mg/kg)					
CK	713.5 ± 6.11	695.5 ± 8.12	480.9 ± 4.28	293.5 ± 2.60	241.7 ± 5.92
US	713.5 ± 6.11	762.5 ± 8.51**	835.5 ± 5.26**	545.4 ± 9.97**	461.4 ± 4.36**
Leu (mg/kg)					
CK	287.3 ± 1.67	197.7 ± 9.06	237.0 ± 4.62	150.6 ± 8.88	138.8 ± 4.41
US	287.3 ± 1.67	216.8 ± 5.51	240.6 ± 7.11	150.1 ± 6.59	146.0 ± 4.03
Met (mg/kg)					
CK	218.2 ± 3.31	180.1 ± 0.98	167.9 ± 4.38	162.2 ± 0.51	155.7 ± 3.36
US	218.2 ± 3.31	180.6 ± 6.95	184.2 ± 2.04*	170.9 ± 1.32*	159.6 ± 1.27
Val (mg/kg)					
CK	218.2 ± 4.91	180.1 ± 5.34	167.9 ± 0.47	162.2 ± 1.26	155.7 ± 3.41
US	218.2 ± 4.91	180.6 ± 6.09	184.2 ± 1.04*	170.9 ± 8.60	159.6 ± 4.78
Tyr (mg/kg)					
CK	146.2 ± 7.92	144.4 ± 0.11	99.46 ± 3.78	50.63 ± 0.18	42.58 ± 5.10
US	146.2 ± 7.92	177.8 ± 3.40*	173.4 ± 8.42**	131.7 ± 7.06**	102.5 ± 5.98**
Arg (mg/kg)					
CK	353.9 ± 3.11	210.4 ± 8.59	158.2 ± 6.73	131.8 ± 3.49	87.94 ± 2.18
US	353.9 ± 3.11	300.9 ± 4.97*	564.5 ± 4.74**	318.9 ± 6.47**	159.2 ± 3.50*
His (mg/kg)					
CK	224.3 ± 4.61	204.0 ± 6.53	140.6 ± 5.74	129.0 ± 1.76	76.08 ± 7.76
US	224.3 ± 4.61	202.0 ± 6.89	204.2 ± 4.38**	185.3 ± 8.22**	142.2 ± 8.38**
Ser (mg/kg)					
CK	3.19 ± 1.03	1.40 ± 0.08	1.24 ± 0.02	1.17 ± 0.01	1.04 ± 0.12
US	3.19 ± 1.03	1.79 ± 0.54	1.26 ± 0.17	1.08 ± 0.03*	1.01 ± 0.04
Glu (mg/kg)					
CK	67.72 ± 2.97	217.0 ± 6.14	348.6 ± 1.98	373.2 ± 2.90	302.9 ± 5.52

Table 3 (continued)

Treatment	Storage time (d)				
	0	4	8	12	16
US	67.72 ± 2.97	61.9 ± 4.16**	91.8 ± 3.44**	157.2 ± 3.93**	51.08 ± 4.83**
Asp (mg/kg)					
CK	249.9 ± 7.36	228.5 ± 8.13	282.1 ± 5.70	418.0 ± 3.08	634.2 ± 6.87
US	249.9 ± 7.36	162.1 ± 5.12	260.2 ± 0.47	264.0 ± 4.12	455.0 ± 4.12

Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

3. Results

3.1. Effect of US treatment on BI and L* values in *L. decastes*

Browning index (BI) is one of important factors used to measure the enzymatic browning rate in fruit and vegetables [21]. The increase of BI was retarded by US treated (Fig. 1A), and a lower level of BI on fruiting body was observed compared with CK treatment, during the entire cold storage. On day 16, the BI of US samples (24.54) was lower than CK samples (31.07). As shown in Fig. 1B, L* value decreased in all samples, and the mushrooms treated with US maintained a higher L* value compared with CK treatment. At day 12, the L* value of US treatment was 77.56 higher than CK samples 69.84.

The sensory quality of *L. decastes* deteriorated during the entire cold storage period (Fig. 1D). On day 8, the CK samples showed obvious browning, the umami taste decreased, and tissue fibrosis increased, while US treated samples showed no obvious change. On day 12, the fruiting body was browning with moderate water loss. However, the US samples were relatively firm, fruiting body was relatively filled, and the typical fresh mushroom flavor was retained. On day 16, CK samples lost the umami taste, the cap was broken, internal tissue fibrosis appeared, there was obvious browning, and the overall acceptance was lower. As shown in Fig. 1C, the US treatment had higher score compared with CK samples in color, smell, texture, condensate inside the crisper, and consumer acceptance on day 16. Above all, the US treatment retarded increases in the BI value, maintained a higher L* value, and the sensory qualities was improved.

3.2. Effect of US treatment on total phenol, flavonoid, and lignin content in *L. decastes*

Total phenol and flavonoid content in plants were related to their antioxidant capacity [22]. Total phenol content increased at the early stage, then decreased during the entire storage time (Fig. 2A). On day 4, the US treatment (20.17 mmol/kg) maintained higher total phenol content than CK samples (7.59 mmol/kg). On day 12, the US treatment had higher total phenol 1.22 times as compared with CK samples. In general, the content of flavonoid was decreased during the entire cold storage. (Fig. 2B). In general, the flavonoid content in the US treatment was higher than CK samples. Lignin content is related to the aging degree of the plant cell wall, and its polymerization prolongs the aging time [23]. The US treatment reduced the increase of lignin accumulation of *L. decastes* (Fig. 2B). On day 12, the mushrooms treated with US (11.47 g/kg) exhibited lower lignin accumulation than the CK samples (21.91 g/kg). Overall, the mushroom treated with US the total phenol and flavonoid consumption was reduced, lignin accumulation was suppressed, maintained high antioxidant capacity, and delayed *L. decastes* fruiting body cell wall aging.

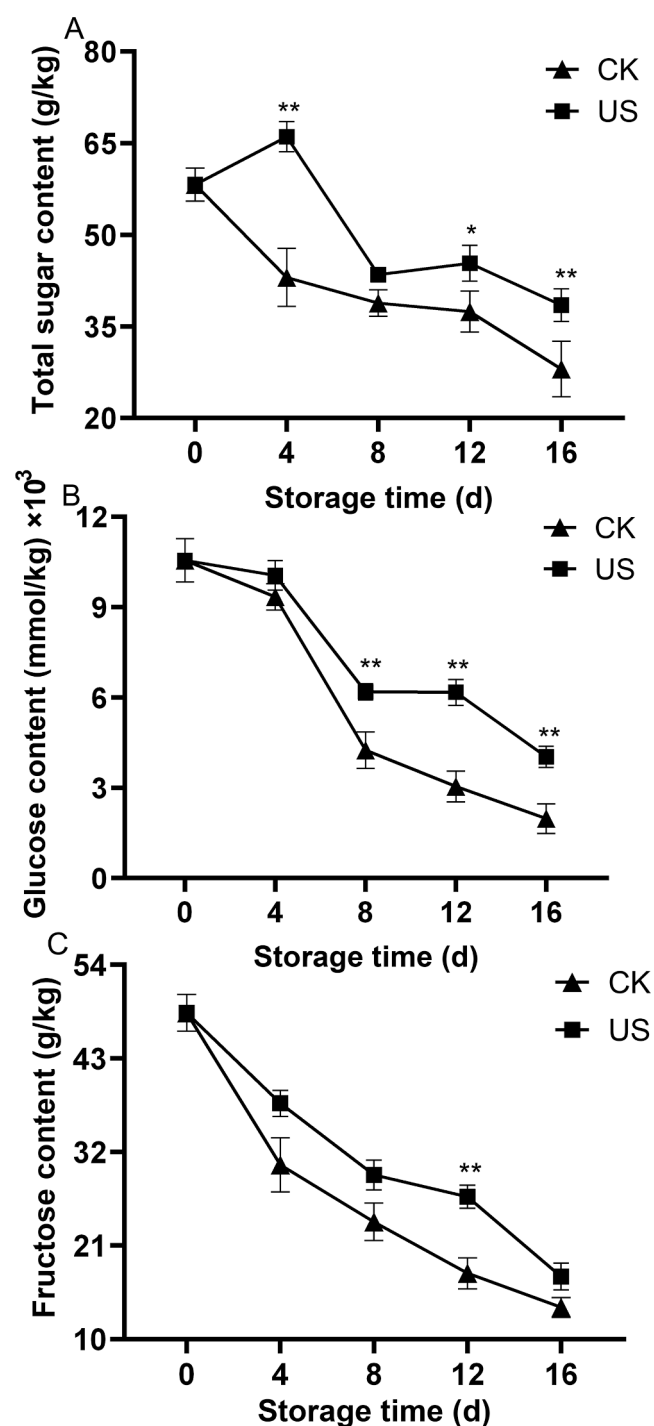


Fig. 5. Effect of US treatment on the content of Total sugar (A), Glucose (B) and Fructose (C) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

3.3. Effect of US treatment on PPO, LOX, CAT, and POD activities in *L. decastes*

PPO is one of the important oxidases related to fruit and vegetable discoloration and reduced storage quality after harvest [4]. In general, CK samples had higher PPO activity compared with US samples during the entire cold storage (Fig. 3A). On day 8, PPO activity of the CK samples (2.58×10^7 U/kg) higher than US samples (1.65×10^7 U/kg). On day 12, PPO activity of CK samples was increased from 1.24×10^7 U/

kg to 3.62×10^7 U/kg significantly higher than US samples 2.72×10^7 U/kg. However, there were only slight differences in PPO activity between US and CK samples on day 16. LOX activity in all mushrooms increased, however, US treatment exhibited significantly lower LOX activity after day 4 (Fig. 3B). LOX activity peak of CK samples (3.45×10^7 U/kg) was higher than that of US samples (1.93×10^6 U/kg) on day 8. Furthermore, LOX activity of US samples lower 38.7 %, 21.0 %, and 66.0 % than CK samples on day 4, day 8 and day 12, respectively. Antioxidant enzymes are related to plant resistance to oxidative stress and can delay fruit and vegetable aging [24]. As shown in Fig. 3C and D, the CAT and POD activities decreased in all samples during the cold storage, the US samples had higher CAT (1.42 times) and POD (2.98 times) activities as compared with CK samples on day 16. US treatment retarded fruiting body enzymatic browning by reducing PPO and LOX activities while maintaining higher CAT and POD activities compared with the CK samples.

3.4. Effect of US treatment on GOGAT and GDH enzymatic activities in *L. decastes*

GOGAT and GDH are involved in nitrogen metabolism and affect glutamate synthesis in plants [25]. The GOGAT activity increased at early stage, then quickly decreased, and the CK samples was higher than the US treatment (Fig. 4A). GDH activity of CK samples was higher than US samples during the entire cold storage (Fig. 4B).

3.5. Effect of US treatment on 11 free amino acid contents in *L. decastes*

The levels of nine free amino acids (Trp, Phe, Leu, Met, Val, Tyr, Arg, His, and Ser) decreased in the CK group compared with that of the US treatment. The US samples had higher Trp (1.38 times), Phe (1.91 times), Tyr (2.41 times), and Arg (1.81 times) contents, as compared with CK samples, on day 16 (Table 3). The Glu content in CK samples was significantly higher than US treated samples during the entire cold storage.

3.6. Effect of US treatment on total sugar, glucose, and fructose contents in *L. decastes*

Sugar is an important substance affecting growth and development and plays an important role in plant respiration and metabolism [26]. The contents of three kinds of sugars decreased during the entire storage at 4 °C (Fig. 5A-C). In general, the total sugar content decreased between US and CK groups, however the total sugar content in US samples was higher than CK samples during the entire cold storage (Fig. 5A). The total sugar content was increased up to 66.07 g/kg by US treatment during the first four days, higher than the CK samples 43.03 g/kg. Glucose provides energy for cells through catabolism and regulates cell aging and death [27]. Glucose consumption flatly decreased during the first four days, followed by a rapid decrease (Fig. 5B). US samples glucose contents higher than CK samples 46.0 %, 103 %, and 103 % on day 8, day 12, and day 16, respectively. The content of fructose was decreased in all samples, on day 12, the US samples fructose content was 26.74 g/kg higher than CK samples 17.74 g/kg, as shown in Fig. 5C. Overall, US treatment retarded the total sugar, glucose, and fructose consumption to maintain the nutritional quality of the *L. decastes* fruiting body.

3.7. Effect of US treatment on ATP, ADP, AMP, NADH, and NAD⁺ concentration and energy charge in *L. decastes*

The ATP and ADP concentration reached a peak during the first four days, and decreased thereafter both the US and CK samples (Fig. 6A-B). On day 4, the ATP concentration by US treatment was 59.99 mg/kg higher than CK samples 51.63 mg/kg, as shown in Fig. 6A. The US samples ADP content was higher than CK samples during the entire cold

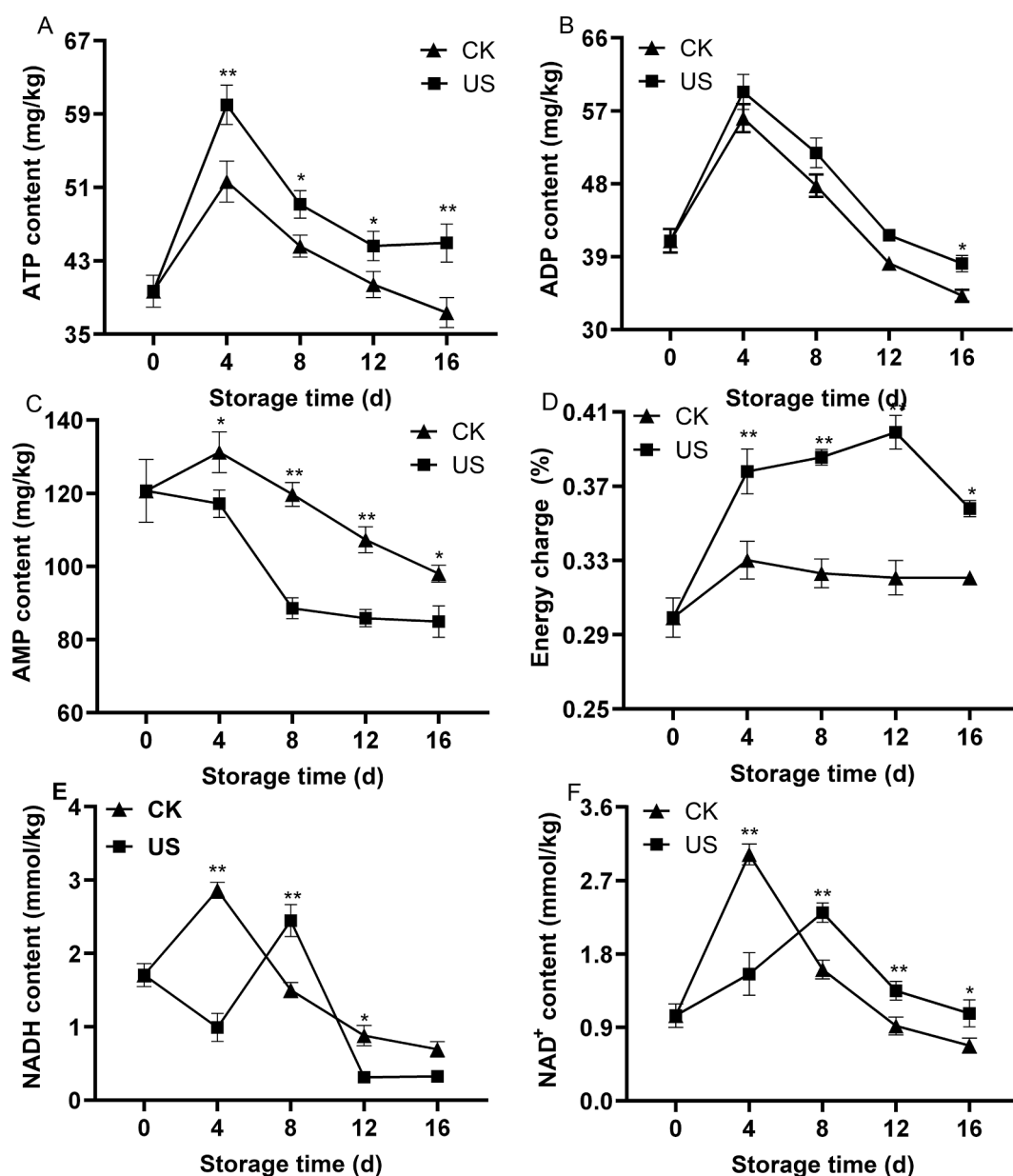


Fig. 6. Effect of US treatment on the contents of ATP (A), ADP (B), AMP (C), NADH (E), NAD⁺ (F) and energy charge (D) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

storage. In general, AMP concentration increased in all samples, during the entire storage period, the US treated samples had lower AMP levels 11.2 %, 35.6 %, 24.6 %, and 15.4 %, as compared with CK on day 4, day 8, and day 12, respectively (Fig. 6C). The fruiting body energy charge of US treated increased, while CK samples slightly changed, and there were significant differences between the two samples during the entire cold storage except for day 16 (Fig. 6D). On day 8, the energy charge of the US treated samples increased from 0.29 to 0.39, was 1.25 times of CK treatment. NADH and NAD⁺ play an important role in energy metabolism, and their concentrations are generally regarded as one of the most important indicator to measure metabolism [28]. In this study, NADH and NAD⁺ contents showed different trends in the two treatments. The NADH content by US treatment decreased during the first four days, then recovered on day 8 to attain the highest value of 2.44 mmol/kg (Fig. 6A). The NAD⁺ content was up to the highest at the same time (Fig. 6B). The US treatment delayed the NADH/NAD⁺ peak levels, as compared with CK samples peaked on day 8, means US treatment can decreased respiration rates. Overall, the US treated fruiting body

maintained higher energy levels and energy charge, decreased the AMP concentration, and retarded NADH and NAD⁺ accumulation.

3.8. Effect of US treatment on CCO, SDH, PFK, and PK enzymatic activities in *L. decastes*

Key respiratory enzymes can improve the regulation of the ripening and aging process by affecting the antioxidant capacity of fruit and vegetables [4]. In general, CCO activity in all mushrooms decreased, however, before the first four days, the mushrooms treated with US exhibited had higher CCO activity, as shown in Fig. 7A. CCO activity was highest on day 4 and US treated samples showed approximately 2.09- and 2.47-times as compared with CK samples on days 8 and 12, respectively. SDH activity rapidly decreased in all mushrooms (Fig. 7B), however, there was a milder decrease by US treatment, as compared with the CK treatment. PFK activity rapidly decreased in all groups, but the activity was higher by US treatment, as compared with the CK treatment during the entire storage period. PFK activity was higher in US

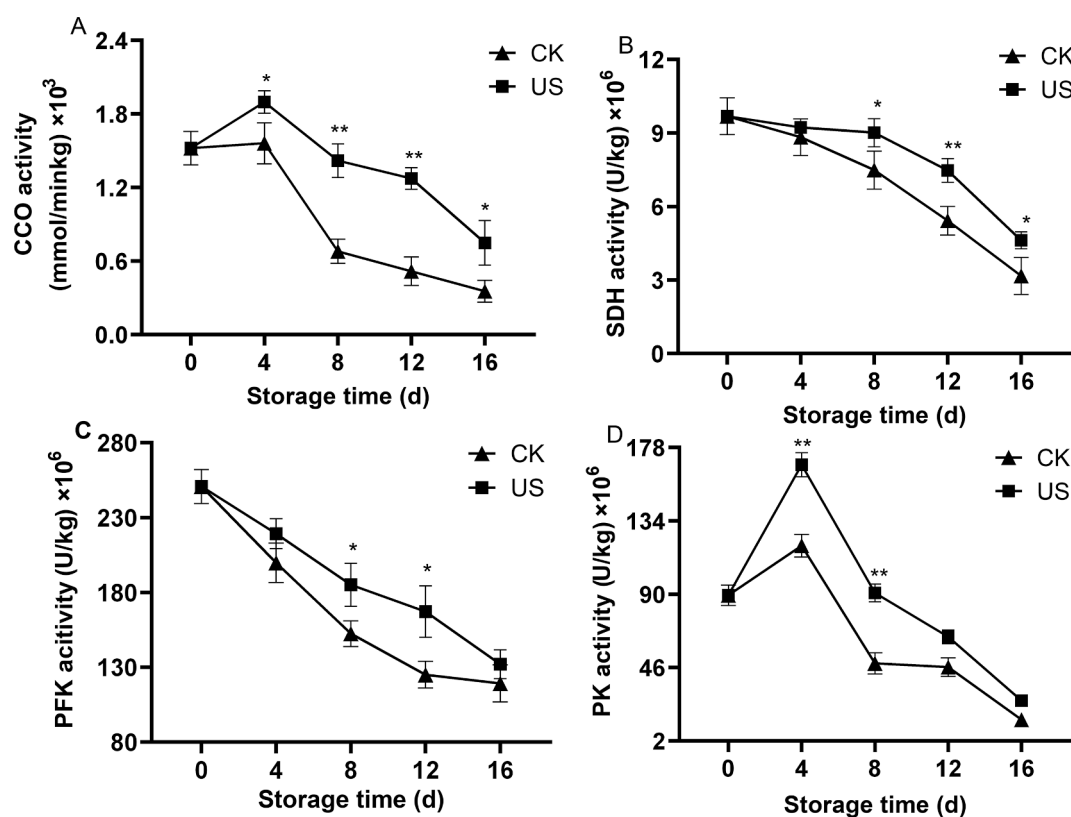


Fig. 7. Effect of US treatment on the activities of CCO (A), SDH (B), PFK (C) and PK (D) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

samples than CK samples 33.8 % on day 12 (Fig. 7C). The US treated samples PK activity was higher than CK samples during the entire storage period (Fig. 7D). On day 4, the PK activity by US treated (1.77×10^6 U/kg) was higher than that of CK samples (1.19×10^6 U/kg). These results showed that the US treated fruiting body maintained higher CCO, SDH, PFK, and PK activity, improved the antioxidant capacity, and retarded the enzymatic browning rate of *L. decastes*.

3.9. Effect of US treatment on *LdPpo1*, *LdPpo2* and *LdPpo3* gene expression in *L. decastes*

PPO gene can affect the enzymatic browning of fruit and vegetables by regulating *PPO* enzyme activity [29]. The US treated fruiting body exhibited a higher L^* value lower BI value and higher total phenol content during the entire cold storage, which may be ascribed to lower *PPO* gene expression and enzyme activity (Fig. 8A-C and 3A). *LdPpo1* and *LdPpo2* genes increased in the two treatments during the entire cold storage period (Fig. 8A and B). On day 16, US treated mushrooms *LdPpo1* and *LdPpo2* expression levels had lower than CK samples 31.8 % and 49.2 %, respectively. *LdPpo3* expression levels were inconsistent between the two treatments (Fig. 8C). The *LdPpo3* expression level slightly increased in all groups, quickly decreased by US treatment lower than CK samples 43.2 % and 44.3 % on day 12 and day 16, respectively.

4. Discussion

Postharvest fruit and vegetables have strong physiological metabolism and high oxidase activity leading to postharvest horticultural product senescence by accelerating the enzymatic browning rate [30]. Browning is an important aspect affecting the shelf life of fruit and vegetables [31]. Reduced oxidase activity improves the storage quality of postharvest horticultural products [32]. The browning index of the US treated samples decreased, and maintained a higher L^* value and

sensory quality compared with CK samples (Fig. 1A-D). Potato browning index is reduced following decreased *PPO* activity (Moon et al., 2020; Zhao et al., 2022) [4,33]. In this study, retarded fruiting body browning index in US treated mushrooms was accompanied by a higher total phenol content (Fig. 2A) which was ascribed to lower *PPO* activity (Fig. 3A), inhibited *LdPpo1* and *LdPpo2* expression, and decreased *LdPpo3* gene expression (Fig. 8A-C). This correlated with previous studies showing that the suppression of *PPO* gene expression and enzyme activity maintains fruiting body whiteness of *A. subrufescens* [34]. These results may be due to that US treatment can reduce the *PPO* enzyme activities by affecting enzyme spatial structure, which were according with Liu et al. [35] and Xu et al. [36] results.

LOX causes cell membrane lipid peroxidation in plants, increased lignin content, and leads to cell wall fibrosis [37]. The mushrooms treated with US retarded *LOX* activity and lignin content (Fig. 3B and 2C), decreased fibrosis and improved the browning phenomenon compared with CK treatment, which may relate with *LOX* gene expression. Zhou et al. [38] found that *Agaricus bisporus* packed with caffeic acid-grafted-chitosan/poly(lactic acid) film can maintain the better storage quality, which may be attributed to the decrease in *LOX* activity and repression of *PuLOX* gene expression. *GOGAT* and *GDH* activities were lower in the US samples than in CK samples which correlated with previous work indicating that inhibition of *GOGAT* and *GDH* activity improves the storage quality of mushrooms [11].

Antioxidant enzymes reduce tissue oxidative damage, delay fruit and vegetable senescence after harvest and maintain high commodity acceptance [7]. *CAT* and *POD* activities reduce intracellular reactive oxygen species and cell apoptosis [39,40]. In this work, mushrooms treated with US maintained higher *CAT* and *POD* activities compared with the CK sample (Fig. 3C and D). Further work is required to determine if this affected the intracellular reactive oxygen species and apoptosis. Higher flavonoid content is related to stronger antioxidant capabilities. A bagging treatment significantly increased *MdLAR* and

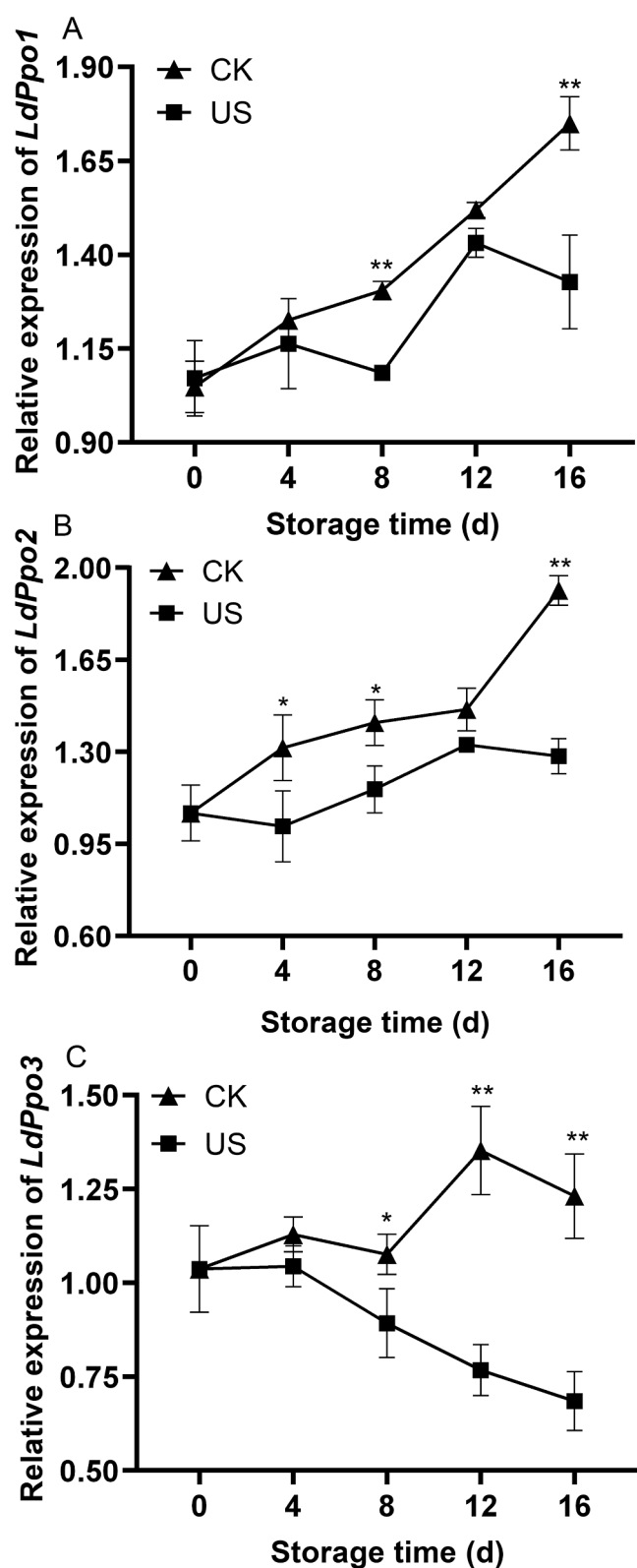


Fig. 8. Effect of US treatment on the expression of *LdPpo1* (A), *LdPpo2* (B) and *LdPpo3* (C) of *Lyophyllum decastes* during 16 days of storage at 4 °C. Within the same storage time, asterisk indicate significant differences (* $p < 0.05$, ** $p < 0.01$).

MdANR expression which retarded the browning index of apple fruit during storage by promoting flavonoid accumulation [41]. In this study, US treatment retained higher flavonoid (Fig. 2B), Trp, Phe, Tyr, and Arg contents (Table 3), and delayed the browning rate of post harvested *L. decastes*. The amino acids assay revealed that the US treatment can significantly retard the Trp, Phe, Val, Tyr, Arg, and His consumption. The contents of Leu, Met, and Val in mushroom after US treatment were higher while the contents of Ser, Asp and Glu content were lower than those in CK samples. Li et al. [42] found that shiitake mushrooms treated with the novel phase change material (PCM) showed higher Phe contents which can decrease the total phenols and flavonoid consumption rate, Meng et al. [43] indicated that Val, Asp, Arg, Thr Met, Leu prevent, the Phe and His had little influence on, and the Ser promote the fresh-cut potatoes browning rate, which was highly similar with this study. The US treatment can maintain the higher levels of Val, Asp, Arg, Thr, Met, Leu, Phe, total phenols, and flavonoid, increased the antioxidant capacity, and reduced the lignin accumulation, further inhibiting the cell wall aging of mushrooms.

In addition, US treated samples had higher total sugar, glucose, and fructose contents (Fig. 5A-C), higher ATP and ADP concentration and energy charge, lower AMP concentration (Fig. 6A-D), and lower NADH and NAD⁺ contents than that of the CK group (Fig. 6E and F). The effect was similar to pre-harvested longan fruit treated with diethyl aminoethyl at 10 mg/kg which retarded the browning rate, decreased NADH and NAD⁺ accumulation, and maintained high energy levels which may be attributed to lower the glycolysis and trichloroacetic acid (TCA) cycle [44]. Longan fruit treated with H₂O₂ had significant browning and lower energy levels [12]. Energy metabolism was associated with enzymatic browning, the Wang et al. [13] found that litchi fruit treated with 0.4 mM melatonin showed increased the energy metabolism related enzymes activities, such as CCO and SDH, leading to maintain higher energy content. Furthermore, energy imbalance was also reported to induced browning in fresh longan [45,46]. Therefore, the US treated fruiting body may maintain a higher energy level, improve the antioxidant capacity, delay the browning rate, and improve the storage quality of post harvested *L. decastes*.

Moreover, we determined the surface bacteria biomass of fruiting body every-four days during the storage. The results are shown that the US treatment can significantly decrease the biomass of surface microbes, as compared with CK treatment. The surface microbe number was up to 6.26 log (CFU/g) in CK group, significant ($p < 0.01$) higher than US group 3.34 log (CFU/g) after day 12 (unpublic data). This result was consistent with Jiang et al. [47] result, which showed the postharvest horticultural products treated with US could reduce the bacteria activity and maintain the storage quality.

As shown in Fig. 9, the US treatment decreased the PPO activity, repressed the expression of *LdPpo1*, *LdPpo2* and *LdPpo3*, and reduced the flavonoid and total phenols consumption. Further, the US treatment maintain higher Val, Asp, Arg, Thr, Met and Leu contents, further increase the antioxidant capacity, and maintain the higher POD and CAT enzymes activities. The US treatment can maintain the activities of key energy metabolism-associated enzymes CCO, SDH, FPK and PK activities, which are responsible for the higher ATP, ADP and EP content in mushroom. Moreover, the LOX activity of mushrooms reduced after US treatment; energy metabolism can regulate the lipid membrane function and decreased the lignin accumulation, ultimately delaying the enzymatic browning of *L. decastes*.

As shown in Table S2, Pearson's r correlation analysis showed that the browning index positively correlated with PPO activity ($p < 0.05$, $r = 0.93$) and significantly negatively correlated with flavonoid content, CAT, and POD activity ($p_{\text{flavonoid}} < 0.05$, $r_{\text{flavonoid}} = -0.88$; $p_{\text{CAT}} < 0.01$, $r_{\text{CAT}} = -0.99$; $p_{\text{POD}} < 0.05$, $r_{\text{POD}} = -0.89$). These results showed that the fruiting body treated with US decreased PPO activity and maintained higher flavonoid content and CAT and POD activities to decrease the enzymatic browning of *L. decastes*. The browning index positively correlated with AMP concentration ($p < 0.05$, $r = -0.91$), and

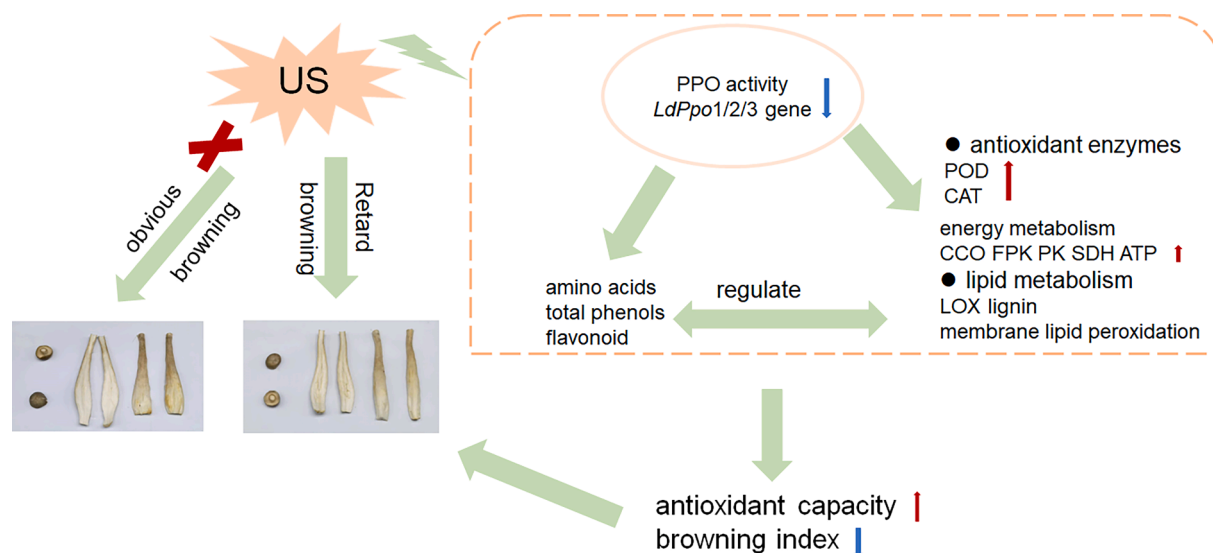


Fig. 9. Proposed mechanism of the browning inhibition of *Lyophyllum decastes* treated with US.

significantly negatively correlated with glucose and fructose content, SDH, and PFK activity ($p_{\text{glucose}} < 0.01$, $r_{\text{glucose}} = -0.96$; $p_{\text{fructose}} < 0.01$, $r_{\text{fructose}} = -0.99$; $p_{\text{SDH}} < 0.05$, $r_{\text{SDH}} = -0.91$; $p_{\text{PFK}} < 0.01$, $r_{\text{PFK}} = -0.99$). These results showed that the fruiting body treated with US maintained lower AMP concentration and retained high SDH and PFK activities to decrease the browning index of *L. decastes* (Table S2). Furthermore, PPO activity of the US treated sample was significantly negatively related to SDH and PFK activity ($p_{\text{SDH}} < 0.01$, $r_{\text{SDH}} = -0.91$; $p_{\text{PFK}} < 0.05$, $r_{\text{PFK}} = -0.9$; Table S2). Overall, the US treatment had decreased oxidase activity, regulated energy metabolism, and decreased fruiting body browning rate which improved the storage quality of *L. decastes*.

5. Conclusion

US treated mushrooms decreased the browning index (fruiting body browning rate), lignin content, and NADH and NAD⁺ content and retarded PPO and LOX activities while retaining higher L* values; POD, CAT, FPK, and PK activities; and total phenol, flavonoid, ATP, and ADP contents compared with CK control samples. This increased the resistance to oxidation and maintained a higher energy level, which improved the storage quality of *L. decastes*.

CRedit authorship contribution statement

Yuxin Hu: Conceptualization, Methodology, Validation, Formal analysis, Supervision, Investigation, Writing – original draft, Writing – review & editing. **Jian Li:** Conceptualization, Methodology, Writing – review & editing. **Hailu Lin:** Conceptualization, Methodology, Writing – review & editing. **Peipei Liu:** Conceptualization, Methodology, Writing – review & editing. **Fangyi Zhang:** Investigation, Resources, Writing – review & editing. **Xiaotong Lin:** Investigation, Resources, Writing – review & editing. **Jiachen Liang:** Investigation, Resources, Writing – review & editing. **Yongxin Tao:** Conceptualization, Methodology, Validation, Formal analysis, Supervision, Investigation, Writing – original draft, Writing – review & editing. **Yuji Jiang:** Conceptualization, Methodology, Validation, Formal analysis, Supervision, Investigation, Writing – original draft, Writing – review & editing. **Bingzhi Chen:** Conceptualization, Methodology, Validation, Formal analysis, Supervision, Investigation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ultsonch.2022.106111>.

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