High hydrostatic pressure as a novel strategy for the simultaneous preservation and enhancement of phenylethanol glycosides in fresh-cut *Cistanche deserticola*

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Abstract: This study introduces high hydrostatic pressure (HHP) as an innovative non-thermal technique to simultaneously enhance preservation and extract phenylethanol glycosides, the primary bioactive compounds in fresh-cut *Cistanche deserticola*. Treatments ranging from 100 to 300 MPa significantly prolonged microbial shelf-life, improved tissue integrity, and increased phenylethanol glycoside yields by up to 34.17%, with optimal accumulation occurring between 9 and 12 d of storage. Microstructural analysis indicated that HHP induced controlled permeability of cell walls, facilitating the release of bioactive compounds without compromising cellular viability. Additionally, HHP stimulated crucial physiological responses such as the activation of phenylalanine ammonia-lyase and enhanced energy metabolism, thereby promoting the biosynthesis and accumulation of the target glycosides. These results illustrate that moderate HHP treatment effectively balances microbial safety, structural quality, and bioactive enhancement, providing a sustainable bioprocessing approach to enhance the value of medicinal plant-based products.

Keywords: *Cistanche deserticola*, high hydrostatic pressure, non-thermal preservation, phenylethanol glycosides, microstructural alteration

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1 Introduction

Cistanche deserticola (Rou Cong Rong), a significant material with medicinal and culinary value, contains phenylethanol glycoside as its key functional component, exhibiting various physiological activities like antioxidation, neuroprotection, and immune regulation[1-3]. However, its susceptibility to spoilage, texture softening, and active component degradation due to high water content and intense post-harvest physiological processes result in an extremely short shelf life[4,5]. Presently, thermal drying is predominantly employed for preservation during production[6]. Despite effectively reducing moisture and microbial growth, high temperatures lead to irreversible destruction of heat-sensitive active components, enzymatic browning acceleration, and tissue structure collapse, severely limiting product value utilization[6]. Consequently, the imperative for the industry's advancement lies in the development of eco-friendly processing technologies that can concurrently ensure quality preservation and vitality retention.

High hydrostatic pressure (HHP) technology, as a non-thermophysical processing method, primarily operates through the reversible effects of pressure on the non-covalent bonds of biological macromolecules, including hydrogen bonds and hydrophobic interactions[7]. This method effectively inactivates microorganisms while preserving the stability of small molecule flavor compounds, pigments, and heat-sensitive nutrients in food[8,9]. Compared to traditional thermal processing, HHP better retains the color, texture, and nutritional quality of fruits and vegetables[10,11]. Recent studies have further indicated that appropriate HHP treatment can induce a mild stress effect on plant tissues. This stress enhances the release of cellular contents by modifying cell membrane permeability and may activate the defense response mechanisms of plant cells[12]. Specifically, it induces the generation of reactive oxygen species signals, which regulate the expression and activity of key enzymes, such as phenylalanine ammonia-lyase (PAL), in secondary metabolic pathways like phenylpropanoid metabolism[13]. Consequently, this process can enhance the targeted synthesis and accumulation of functional components while preserving the integrity of the food. These findings suggest that

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HHP functions not merely as a passive preservation tool but also as a potential active strategy for biological processing.

High hydrostatic pressure (HHP) has shown potential for preserving and enhancing quality in certain fruits and vegetables, yet its exploration in medicinal plants, particularly fresh-cut *Cistanche deserticola* products, remains limited. The existence of a stress-dependent optimal preservation window induced by HHP treatment on *Cistanche deserticola*, along with the accumulation of bioactive compounds, remains uncertain. The intricate physiological response network, including oxidative stress, energy metabolism, membrane integrity, and fluctuations in the phenylpropane metabolic pathway, collectively governs the ultimate quality and functional outcomes. Of paramount importance is determining whether the stress response triggered by HHP can synergistically enhance preservation and activation in *Cistanche deserticola*. It is crucial to discern the fundamental disparities between this stress response mechanism and the damage response elicited by thermal processing. Addressing these inquiries is imperative for precise regulation and widespread industrial implementation of HHP technology.

This study aims to systematically analyze the effects of different pressure intensities of High Hydrostatic Pressure (HHP) treatment on the quality stability and phenylethyl alcohol accumulation dynamics of fresh-cut *Cistanche deserticola* during storage. By conducting microscopic structure observations and analyzing physiological indices such as oxidative stress, energy metabolism, and key enzyme activities, the study elucidates the physiological mechanisms through which HHP treatment influences the quality and functional components of *Cistanche deserticola*. The core hypothesis proposed is that there is a moderate range of HHP pressure (e.g., 100-500 MPa) within which treatment can induce reversible changes in membrane permeability, preserve cell structure integrity, and activate defense metabolic responses mediated by reactive oxygen species signals. This process enables the effective preservation of storage quality and targeted enrichment of phenylethanol glycosides. This research aims to establish a theoretical foundation and procedural guidelines for the high-quality non-thermal processing of HHP technology in medicinal and edible plant materials.

2 Materials and methods

2.1 Materials

Fresh *Cistanche deserticola*, approximately 3 years old, 30-40 cm long, and 5-7 cm in diameter were collected in autumn from Alxa, Inner Mongolia Autonomous Region. The samples were transported under refrigeration and processed upon arrival. Echinacoside (98% pure), verproside (98% pure), cistanoside A (98% pure), and isomucronatus glycoside (98% pure) were sourced from Chengdu Desite Biological Technology Co., Ltd. (Chengdu, China). Hydrogen peroxide and ATP quantification kits were obtained from Yuanye Biotechnology Co., Ltd. (Shanghai, China) and Yuchun Biotechnology Co., Ltd. (Shanghai, China), respectively. Methanol and acetonitrile of HPLC grade were used for chromatographic analysis, while all other chemicals were of analytical grade.

2.2 Fresh-cut *Cistanche deserticola* slices preparation and HHP treatment

Raw *Cistanche deserticola* slices were harvested from the field and transported to the laboratory under low-temperature conditions. Subsequently, the slices were washed immediately with running water to remove adhering soil and scale leaves, followed by gentle blotting with absorbent paper to eliminate surface moisture. The cleaned roots were then mechanically sliced into uniform 4 mm thick pieces. A total mass of approximately 50 g of *Cistanche deserticola* slices was randomly divided into four packages, each placed in polyamide/polyethylene (PA/PE) vacuum bags. A vacuum machine (DZ400-2D, Wenzhou Huaneng Co., Ltd., Wenzhou, China) was employed to evacuate the air from the bags. Three packages of *Cistanche deserticola* slices were subjected to pressurization using water as a medium in a 6.2 L-capacity high hydrostatic pressure (HHP) apparatus (HHP-600, Bao Tou KeFa High Pressure Technology Co., Ltd., Baotou, China) at pressures of 100 MPa, 300 MPa, and 500 MPa, respectively. Typically, less than 2 min of pressurization is required to achieve the set pressure, with 3 s needed to release the pressure. The *Cistanche deserticola* slices in the three packages were pressurized for 15 min at 37°C. The heat-treated *Cistanche deserticola* slices, which were steamed for 5 min and served as the experimental groups, and the untreated slices served as the control group. All groups were stored in a refrigerator at 4°C. The determination of each index was conducted separately during the 21-day storage period. The whole experimental flowchart is shown in Figure 1.

2.3 Microstructure analysis

2.3.1 Neutral red staining (NRS)

A neutral red staining solution was prepared by dissolving 0.5 g of neutral red powder in 50 mL of Ringer's solution at 30°C-40°C, followed by filtration. *Cistanche deserticola* slices were fully immersed in the staining solution for a set period. Post-staining, the slices were delicately rinsed with Ringer's solution to eliminate surplus dye. Subsequently, microscopic observation was promptly conducted, and representative images were captured for analysis.

2.3.2 Scanning electron microscopy (SEM)

The surface and microstructure of *Cistanche deserticola* slices were analyzed using a scanning electron microscope (Hitachi TM4000, Japan). Prior to analysis, the samples were gold-plated, and then the observations were conducted under high vacuum conditions at an accelerating voltage of 15 kV. Representative images were captured at a magnification of 200×.

2.4 *Cistanche deserticola* slices quality assessment

2.4.1 Determination of appearance and color

Photographs of *Cistanche deserticola* slices were captured using an iPhone 15Pro. The color parameters (L^*, a^*, b^*) of the slices were assessed with a portable handheld color difference meter (CR-20, Japan) as outlined by Borah[14]. Five random spots on each sample were evaluated to determine average values for subsequent statistical analysis.

2.4.2 Determination of weight loss and hardness

Weight loss was determined gravimetrically according to reference[15]. The rate of weight loss was expressed as the percentage loss (%) of the sample mass relative to the initial weight of *Cistanche deserticola* slices, which were washed and dried. Hardness analysis of *Cistanche deserticola* slices (1 cm×1 cm) was conducted using a texture analyzer (TA.XT Plus, Stable Micro Systems, UK) equipped with a P/2 probe, in accordance with the described method. The test conditions were established as follows: pre-test speed of 1 mm/s, test speed of 2 mm/s, post-test speed of 5 mm/s, and a trigger force of 5 g.

2.4.3 Microbiological analysis

Microbial loads of *Cistanche deserticola* slices were evaluated using the method described by reference[16]. Briefly, samples (2.5 g) were aseptically homogenized with 22.5 mL of 0.1% peptone water for 2 min. Serial decimal dilutions were then prepared in peptone

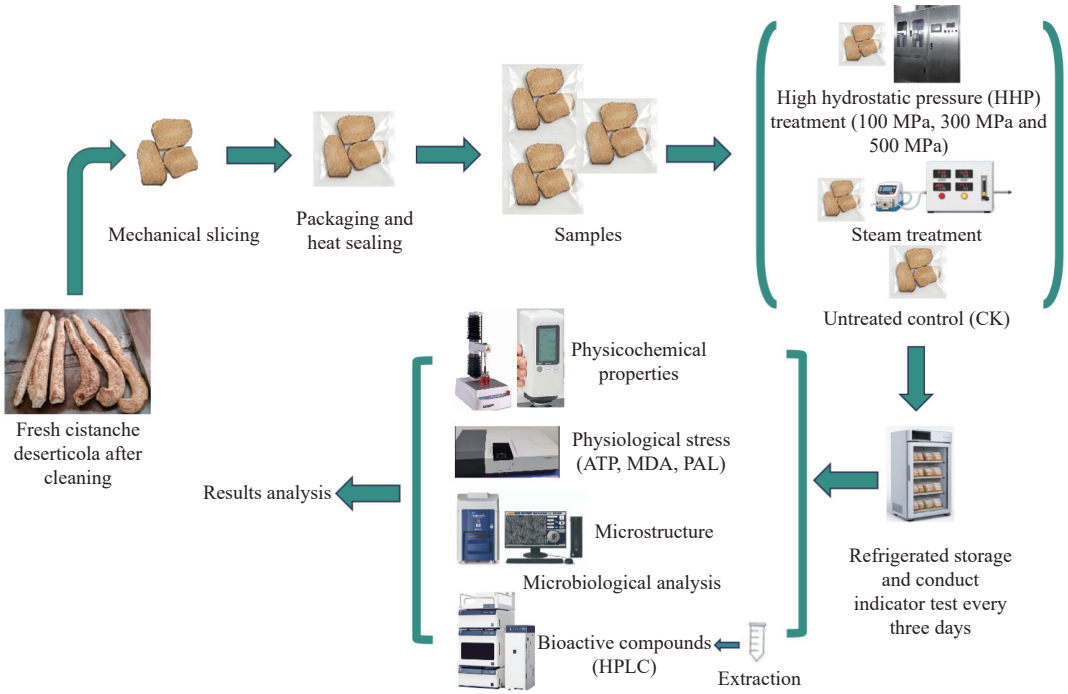


Figure 1 Experimental flowchart

water. Subsequently, 1 mL of the microbial gradient dilutions was pour-plated onto plate count agar and potato dextrose agar to determine total viable counts (TVC). The plates were incubated at 37°C for 48 h. The results were expressed as log CFU/g.

2.5 Measurement of physiological stress

2.5.1 Respiratory intensity

Respiratory intensity was determined using a gas analyzer (CheckPoint3, Dansensor®, AMETEK MOCON, USA) according to the method[17] with modifications. Briefly, samples (50 g) were enclosed in a sealed vessel and incubated at room temperature for 2 h. Subsequently, the CO_2 concentration (%) in the headspace was quantified to determine the respiratory intensity (RI) using the formula as follows:

$$\mathrm{RI}(\mathrm{CO_2},\mathrm{mg/kg\cdot h}) = \frac{[V\times\varphi\times M\times 1000]}{(V_0\times m_0\times t)}\times 100 \quad (1)$$

where, V represents the total volume of the sealed container, mL; φ is the CO_2 concentration in the headspace of the sealed container, %; M is the molar mass of CO_2 (44 g/mol); V_0 is the molar volume of CO_2 (22.4 L/mol); m_0 is the mass of the sample, g; t is incubation time, h.

2.5.2 ATP content

ATP levels in *Cistanche deserticola* slices from different treatment groups were measured using a commercial ATP content assay kit, adhering rigorously to the manufacturer's guidelines. The determination of Malondialdehyde (MDA) content was conducted.

2.5.3 Malondialdehyde (MDA) content

The MDA content was determined according to the method described by Wang et al. (2024) with slight modifications[18]. Briefly, samples (2 g) were homogenized with 5 mL of 10% (w/v) trichloroacetic acid (TCA) and a small amount of quartz sand. The resulting homogenate was centrifuged at 12 000 ×g for 20 min at 4°C. Then, 1.0 mL of the supernatant was mixed with 1.0 mL of 0.67% thiobarbituric acid (TBA) solution and heated in a boiling water bath for 20 min. After cooling, the mixture was centrifuged at 10 000 ×g for 20 min at 4°C. The absorbance of the resultant supernatant was measured at 450, 532, and 600 nm, respectively. A blank was prepared by substituting the sample extract with 1.0 mL of 10% TCA solution.The MDA content was then calculated using the formula as follows:

$$\mathrm{MDA}(\mu\mathrm{mol/L}) = \frac{[6.45\times(\mathrm{OD_{532}}-\mathrm{OD_{600}})-0.56\times\mathrm{OD_{450}}]\times V}{V_S\times m} \quad (2)$$

OD_{532}, OD_{600}, and OD_{450} represent the absorbance values at the wavelength of 532 nm, 600 nm, and 450 nm, respectively; V is the total volume of the extract solution, mL; V_s is the volume of supernatant used for reaction, mL; m is the fresh weight of the sample, g.

2.5.4 Relative conductivity

The relative conductivity of *Cistanche deserticola* slices was measured using the method described by reference[18] with modifications. For each sample, 10 g was immersed in 20 mL of deionized water and incubated at 25°C for 30 min. The initial conductivity (γ_1) of the solution was measured with a conductivity meter. Subsequently, the sample was boiled for 30 min, cooled rapidly to room temperature, and the final conductivity (γ_0) was recorded. The relative conductivity was calculated as follows:

$$\gamma = \frac{\gamma_1}{\gamma_0}\times 100\% \quad (3)$$

2.5.5 H_2O_2 content

The H_2O_2 content in *Cistanche deserticola* slices was determined using a commercial assay kit, following the method of reference[19] with minor modifications. Briefly, samples were homogenized in 5 mL of ice-cold acetone and then centrifuged at 12 000 ×g for 20 min at 4°C. The resulting supernatant was collected for H_2O_2 quantification according to the manufacturer's instructions.

2.5.6 Activity of phenylalanine ammonia-lyase (PAL)

PAL activity was assessed according to the method of reference[20]. Briefly, a sample (4 g) was homogenized in 16 mL of phosphate buffer (pH 8.8) containing 0.4 g of polyvinylpyrrolidone (PVP). The homogenate was then centrifuged at 10 000 ×g for 20 min at 4°C, and the resulting supernatant was collected as the crude enzyme extract. For the assay, 0.5 mL of the extract was mixed with 2 mL of phosphate buffer (pH 8.8) and 2 mL of a 0.02 mol/L L-phenylalanine solution. The mixture was incubated at

30°C for 30 min, after which the reaction was terminated by the addition of 0.5 mL of 0.6 mol/L HCl. The absorbance at 290 nm was measured before and after incubation, and the difference in absorbance was utilized to calculate PAL activity.

2.6 Determination of phenylethanol glycosides of *Cistanche deserticola* slices

2.6.1 Chromatographic conditions

Phenylethanol glycoside compounds were analyzed using high-performance liquid chromatography (HPLC). The analyses were performed with a Hitachi HPLC instrument (Hitachi HPLC Instruments Co., Ltd., Dalian, China), which included an 8 μL injector loop, a solvent delivery module (PM1110 LPGR(C)) with a double plunger reciprocating pump, and a PM1430(C) UV detector. Separation was carried out on a LaChrom C_{18} column (250 mm× 4.6 mm, 5 μm). The mobile phase consisted of solvent A (acetonitrile) and solvent B (0.5% formic acid, v/v). The gradient elution was as follows: initial 0-9 min, A(10%-19%); 10-31 min, A(19%-22%); 32-44 min, A(22%-25%); 45 min, A(25%-10%); 46-50 min, A(10%). The UV absorption was monitored at 320 nm. The column temperature was maintained at 30°C, and the flow rate was set at 0.6 mL/min.

The stock solution containing four reference standards echinacoside, verproside, cistanoside A, and isoacteoside was prepared by dissolving these standards in 50% methanol. Then, the stock solution was diluted to appropriate concentrations to establish calibration curves. These curves were constructed using six concentration levels (0.05-10.0 mL of standard solution diluted to 10 mL). Peak areas were plotted against concentration to derive linear regression equations (Table 1).

Table 1 Linear regression equation of each standard

Standard	Linear regression equation	R^2
Echinacoside	Y=1×10^7x–789.51	0.9997
Verproside	Y=1×10^7x+4133.9	0.9996
Cistanoside A	Y=1×10^7x–3219.7	0.9997
Iso Trichosanthin	Y=1×10^7x+7587.7	0.9995

2.6.2 Sample preparation

The dried powders of the samples (5 g) were accurately weighed and extracted via ultrasonication using 15 mL of a 50% aqueous methanol solution for 2 h. Then, the resulting mixture was adjusted to the original weight, and aliquots of the supernatant were filtered through a 0.45 μm membrane prior to HPLC injection.

2.6.3 Determination of phenylethanol glycosides

Based on the standard curves established above, this study analyzed the extraction amounts of the four primary phenylethanol glycosides from *Cistanche deserticola* slices under different treatments. The total extraction amount of phenylethanol glycosides is equal to the sum of the contents of echinacoside, verproside, cistanoside A, and isoacteoside. The calculation for the four main phenylethanol glycosides is as follows:

$$X(\mathrm{mg/g}) = \frac{\rho \times V}{m} \times f \quad (4)$$

where, X represents the content of echinacoside, verproside, cistanoside A, and isoacteoside, respectively, mg/g; ρ is the concentration of standards in extract solution, mg/mL; V is the volume of extract, mL; m is the weight of samples, g; and f is the dilution factor.

2.7 Statistical analysis

All experiments were performed in triplicate, and data are expressed as the mean±standard deviation. Statistical analyses were conducted using OriginPro 2021 (OriginLab, USA) and IBM SPSS Statistics (SPSS Inc., USA). One-way analysis of variance (ANOVA) followed by Tukey's post hoc test was used to identify significant differences at a 95% confidence level (p<0.05).

3 Results and discussion

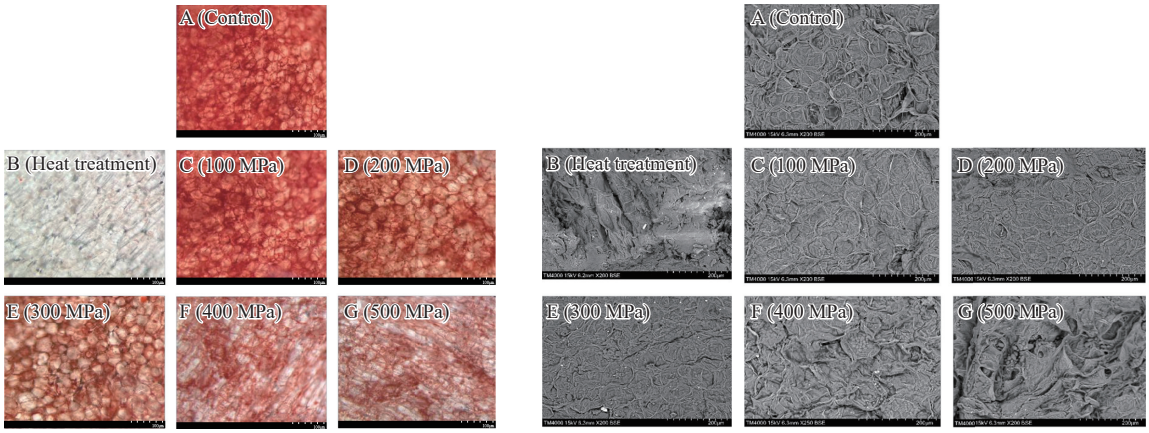
3.1 Neutral red dye (NRD)

Untreated *Cistanche deserticola* slices displayed intense red staining and distinct shapes, indicating the presence of numerous viable cells with intact membranes (Figure 2a). In contrast, heat-treated samples appeared nearly white, indicating significant cellular damage due to thermal degradation. These findings align with prior research on thermally processed plant tissues, such as red dragon fruit and black rosehip, which also exhibited structural collapse and membrane disintegration following heat treatment[21,22]. After HHP treatment, there was a notable development of incomplete cell membranes, accompanied by a substantial decrease in overall red staining. Samples treated at 100 MPa exhibited staining intensity comparable to the control group, indicating minimal cellular damage. With an increase in pressure from 200 to 500 MPa, the red color gradually diminished, indicating a progressive decline in membrane integrity. This pattern suggests that despite being classified as a non-thermal technology, HHP can exert mechanical stress on cellular structures, resulting in membrane permeabilization at elevated pressures[7]. Similar structural alterations have been observed in yam slices, where tissue cracking became apparent at pressures exceeding 200 MPa and intensified with increasing pressure[23]. These findings indicate that high hydrostatic pressure (HHP) treatment, particularly at levels above 300 MPa, significantly impacts the integrity of cell membranes in *Cistanche deserticola* slices, albeit to a lesser degree than thermal treatment.

3.2 Scanning electron microscopy (SEM)

The microscopic structure of *Cistanche deserticola* slices was analyzed using scanning electron microscopy (SEM) at a magnification of 200× (Figure 2b). The untreated group displayed a tightly organized and morphologically intact tissue structure. In contrast, heat treatment induced significant structural collapse, leading to a complete loss of the original morphology. This observation aligns with the findings of reference[6], who attributed the damage to starch gelatinization and solubilization during heating. HHP treatment induced pressure-dependent microscopic alterations. At 100 MPa, the tissue largely retained its integrity, resembling the control. However, as pressure increased to 300 MPa, the thickness of the outer tissue wall diminished, although the overall morphology was preserved. This observation is consistent with the results of neutral red staining and reinforces the notion that low-pressure HHP treatment results in minimal structural damage, a finding also observed in yam slices[23]. An additional pressure increase to 400 MPa resulted in tissue rupture and a disorganization of the cellular arrangement. At 500 MPa, significant deformation and strong adhesion of the damaged tissues were noted. These observations align with findings from studies on HHP-treated edamame, which documented enhanced surface roughness, porous structures, and a stacked fiber arrangement under high pressure[24]. The structural modifications result from the influence of HHP on non-covalent bonds, including hydrogen bonds and hydrophobic interactions, which are essential for preserving cell membrane integrity. Moreover, elevated pressure can induce functional group reorganization, resulting in the breakdown of plant cell walls and the liberation of polymers with diverse solubilities, as documented

in alternative botanical contexts[25]. These alterations at the microstructural level elucidate the concomitant physiological and physicochemical changes evident in *Cistanche deserticola* slices treated with high hydrostatic pressure.



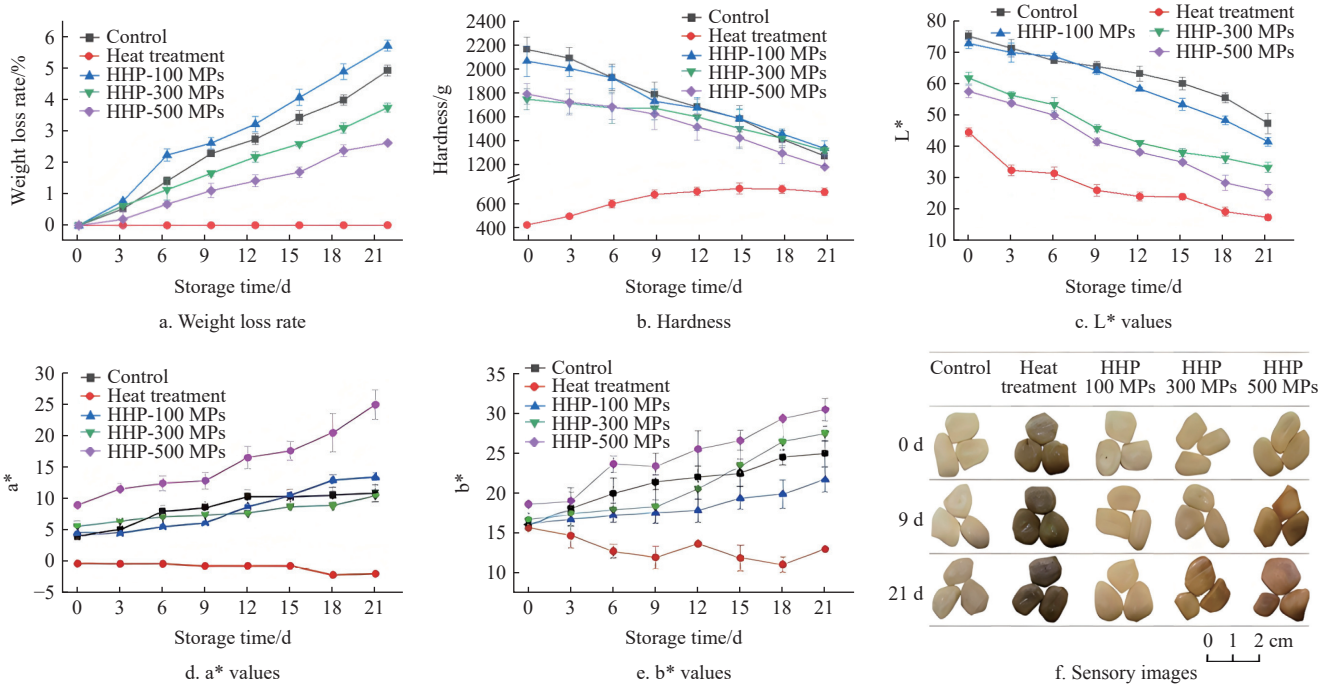
a. Neutral red staining images b. Scanning electron microscopy images

Figure 2 Neutral red staining images and scanning electron microscopy images of the tissue structure of *Cistanche deserticola* slices at 200×

3.3 Physicochemical properties

3.3.1 Color and appearance

As illustrated in Figure 3c-3e, both heat and high hydrostatic pressure (HHP) treatments significantly affected the color parameters (L^*, a^*, b^*) in comparison to the control. Throughout the storage period, L^* values declined across all groups, whereas a^* and b^* values typically increased, reflecting a gradual darkening and yellowing of the samples. Meanwhile, heat treatment resulted in the most significant decrease in L^* values, along with the lowest a^* and b^* values ($p<0.05$), indicating considerable color deterioration due to thermal-induced pigment degradation and non-enzymatic browning[26]. In samples subjected to the HHP treatment, it was observed that the color changes were dependent on the applied pressure. At 100 and 300 MPa, the reductions in L^* and the increases in a^* and b^* were moderate, suggesting improved color retention compared to heat treatment. This phenomenon may be attributed to limited membrane disruption and a slower rate of oxidation under moderate pressure. In contrast, treatment at 500 MPa resulted in significantly higher a^* and b^* values ($p<0.05$), shifting the color toward yellow-red (Figure 3d-3f). The intense color changes observed in HHP treatment are likely attributable to significant damage to the integrity of cell and vacuole membranes caused by extremely high pressure[27]. This disintegration of the membrane system results in the substantial release of pigments, such as flavonoids and anthocyanins, which were previously distributed regionally. Their interaction with polyphenol oxidase, peroxidase, and other enzymes triggers rapid enzymatic browning and pigment oxidation[28].



a. Weight loss rate b. Hardness c. L* values

d. a* values e. b* values f. Sensory images

Figure 3 Changes in weight loss rate (a), hardness (b), color (c-e), and appearance (f) of *Cistanche deserticola*

3.3.2 Weight loss rate

As illustrated in Figure 3a, the weight loss rate increased significantly over the storage period in both the control and HHP-treated groups ($p<0.05$). In contrast, the heat-treated group exhibited the lowest weight loss rate, which remained relatively stable throughout storage. This is likely attributed to protein denaturation

and the formation of a cross-linked network that impeded moisture migration. At 100 MPa, weight loss significantly exceeded that of the control group (p<0.05), likely due to enhanced respiratory metabolism and increased transpiration under moderate pressure, consistent with the elevated respiration. At pressures of 300 MPa and 500 MPa, weight loss rates fell below those of the control group on day 6. By day 21, the groups subjected to 300 MPa and 500 MPa demonstrated reductions of 24.05% and 53.37%, respectively, compared to the control. The mitigation of water loss observed at 300 MPa may be associated with the concurrent effects of suppressed respiratory activity and the development of a more compact tissue structure, which could enhance the moisture barrier. This interpretation is consistent with reports where high-pressure-induced tissue compaction contributed to reduced water loss in yam slices.

3.3.3 Hardness

The initial hardness of untreated *Cistanche deserticola* slices was 2169 g, as illustrated in Figure 3b. Following heat treatment, the hardness significantly decreased to 700 g (p<0.05), exhibiting a continuous decline throughout storage. This softening phenomenon is ascribed to thermal-induced cell damage and moisture loss[29]. HPP at 100 MPa did not significantly impact the initial hardness compared to the control (p>0.05). Conversely, treatments at 300 MPa and 500 MPa led to notably reduced hardness (p<0.05). Consistent with previous observations in HHP-treated yam slices, its softening is due to the mechanical damage to the cell wall caused by high pressure, as well as the enzymatic and non-enzymatic conversions of the cell wall polysaccharides[23]. A noteworthy phenomenon is that the difference in hardness between the high-pressure treatment groups, particularly the 300 MPa group, and the control group diminished over extended storage periods. By days 15 to 21, the hardness of the 300 MPa group was no longer significantly different from that of the control group (p>0.05). This observation implies that the storage process mitigated the initial softening effect induced by high-pressure treatment. A similar trend was documented by previous study on mango, which found that the softening resulting from HHP treatment became negligible in the later stages of storage[30]. Their research suggested that appropriate HHP treatment may influence texture by modulating the activities of enzymes related to cell wall modification, such as pectin methylesterase (PME). PME facilitates the demethylesterification of pectin, thereby creating conditions conducive to the formation of calcium cross-linkages that enhance firmness. Consequently, we hypothesize that the 300 MPa treatment in the present study may function as a mild stressor. This process may help maintain a hardness level comparable to that of the control group during the middle and later storage periods. In contrast, the 500 MPa treatment inflicted excessively severe initial damage, rendering the repair mechanisms insufficient to achieve full compensation.

3.3.4 Total colony count

The total colony count, illustrated in Figure 4, exhibited a consistent increase with storage duration across all experimental groups. However, the rate of increase slowed after 9 days, likely due to the gradual depletion of available carbohydrates. The control group exceeded the hygienic threshold (6.01 lg CFU/g) by day 9, reaching 6.51 log CFU/g by day 12. In the HHP-treated groups, microbial growth was effectively suppressed in a pressure-dependent manner. At 100 MPa, the colony count surpassed the hygienic limit by day 12, with no significant difference from the control group (p>0.05). The colony growth curve for the 100 MPa treatment group coincided with that of the control group until surpassing the safety limit on the 12th day. This observation suggests that this pressure intensity was ineffective in inhibiting microbial growth. The lack of efficacy may be attributed to the fact that 100 MPa induces only sublethal damage to microbial cells, resulting in reversible alterations in membrane permeability or transient metabolic dysfunction. Consequently, the damaged cells are capable of repair and can continue to proliferate throughout the storage period. In contrast, samples treated at 300 MPa and 500 MPa remained below the threshold throughout the 18-day storage period, exhibiting significant microbial inhibition compared to the control (p<0.05). This stress-dependent antibacterial effect can be elucidated by the stress-mediated cell death mechanism described by Liu et al[31]. When pressure reaches 300 MPa or higher, it can inflict irreversible damage on the structure and function of the microbial cell membrane, resulting in the leakage of intracellular electrolytes and essential substances. Furthermore, this pressure may lead to the denaturation and inactivation of enzymes involved in energy metabolism, causing metabolic paralysis in the cells. At even higher pressures, such as 500 MPa, damage to genetic material (DNA) may occur, which is typically irreparable and serves as a critical factor directly contributing to cell apoptosis. In this study, the 500 MPa treatment group exhibited the most pronounced antibacterial effect, consistently yielding the lowest colony count. This outcome is likely attributable to the simultaneous induction of all aforementioned severe damages, particularly the destruction of genetic material, thereby achieving the most comprehensive microbial inactivation.

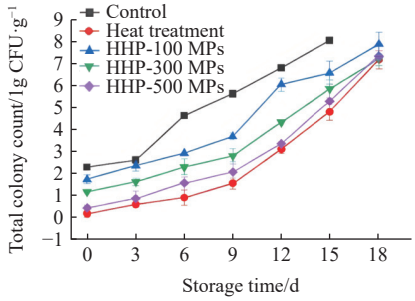


Figure 4 Changes in total colony count of *Cistanche deserticola* slices caused by different treatment

3.4 Physiological stress index

3.4.1 Respiratory intensity

As shown in Figure 5a, significant differences were observed in the effects of various treatments on the respiratory intensity of fresh-cut *Cistanche deserticola*. Following heat treatment, the respiratory intensity of the *Cistanche* slices became undetectable, indicating that high temperatures resulted in the complete cessation of cellular metabolic activities. In all experimental groups, the respiratory intensity of the *Cistanche* slices initially increased during storage, peaked around the 3rd day, and subsequently declined as storage time extended. The trend in respiratory intensity for the 100 MPa pressure treatment group did not differ significantly from that of the control group (p>0.05). This finding aligns with the research conducted by Feng et al.[32], which demonstrated that relatively low-pressure treatments did not significantly affect the respiratory intensity of green asparagus. This suggests that this pressure level may not have inflicted sufficient shock or damage to the cellular metabolic system to alter its operational intensity. Treatments at 300 MPa and 500 MPa significantly inhibited respiratory intensity, with values consistently lower than those of the control group and the 100 MPa treatment group throughout the storage period. This

observation aligns with findings by Sun et al.[33] regarding fresh-cut *Gastrodia elata*, which indicated that higher pressure treatments (300 MPa) effectively suppress product respiration. The reduction in respiratory intensity primarily results from the physical disruption of cell structures, including mitochondrial membranes, and respiratory enzyme systems due to elevated pressure. Such pressure can alter membrane permeability, modify enzyme conformation, or obstruct substrate channels, thereby directly inhibiting the efficiency of the electron transport chain and related metabolic pathways, ultimately reducing the overall metabolic rate. Notably, the 500 MPa treatment, while initially causing significant physical damage (as evidenced by SEM results), may induce a transient stress metabolism. However, this is followed by severe impairment of cellular function, as indicated by the sustained suppression of respiratory intensity at a low level. In conclusion, the respiratory intensity data clearly demonstrate that the effects of high hydrostatic pressure (HHP) treatment are stress-dependent. HHP treatment at 100 and 300 MPa significantly reduced respiratory intensity (p<0.05), thereby effectively suppressing metabolic activity at moderate pressure levels and potentially extending shelf life.

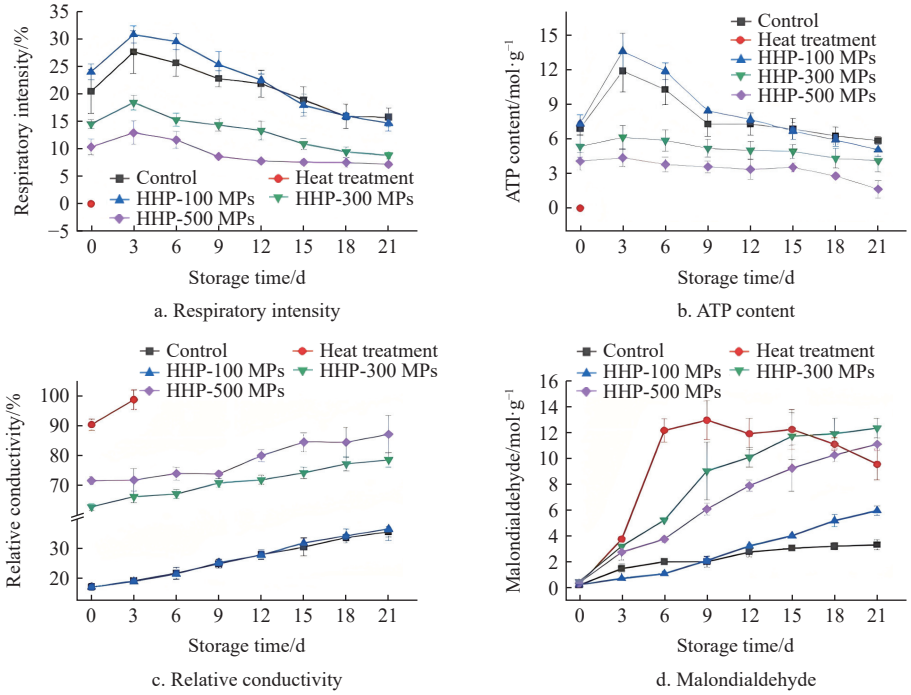


Figure 5 Changes in respiratory intensity (a), ATP content (b), relative conductivity (c), and Malondialdehyde (d) of *Cistanche deserticola* slices caused by different treatment

3.4.2 Adenosine triphosphate (ATP) content

As shown in Figure 5b, the ATP levels in *Cistanche deserticola* slices exhibited significant variations among different groups. In both the control and 100 MPa HHP-treated groups, ATP content initially increased and then gradually decreased over time (p<0.05). Remarkably, the ATP contents in the 100 MPa group consistently surpassed that of the control group, indicating that moderate HHP stress could potentially boost energy metabolism and promote ATP production under mild stress conditions. Heat treatment led to undetectable ATP levels (p<0.05), aligning with the complete suppression of respiratory intensity in Figure 5a, indicating severe cellular damage and metabolic arrest. Similarly, HHP treatments at 300 MPa and 500 MPa resulted in significantly lower ATP contents compared to the 100 MPa group (p<0.05), likely due to physical disruption of mitochondrial membranes and impairment of the respiratory chain under high pressure, thereby restricting the conversion of sugars into ATP[34]. As the storage time increased, ATP content decreased in all groups, indicating a gradual depletion of cellular energy reserves. This observation is consistent with previous studies on longan and pummelo fruits, where ATP degradation was closely associated with senescence and quality deterioration[35].

3.4.3 Relative conductivity

The variations in relative conductivity of fresh-cut *Cistanche deserticola* slices primarily reflect changes in cell membrane integrity. As illustrated in Figure 5c, at day 0, the electrolyte leakage of control *Cistanche deserticola* slices was 16.94%, which was significantly elevated to 90.33% following heat treatment (p<0.05), indicating extensive tissue damage. The conductivity exhibited pressure-dependent increases with HHP treatment. At 100 MPa, no significant difference was observed compared to the control (p>0.05), suggesting minimal membrane damage at this low pressure. However, at 300 MPa, the conductivity rose to 62.69%, further increasing to 71.52% at 500 MPa (p<0.05). Increased membrane permeability results in the leakage of intracellular electrolytes, including inorganic ions, such as K^+, Na^+, Ca^{2+}, as well as small organic molecules like soluble sugars and organic acids, thereby leading to an increase in conductivity. As illustrated in Figure 5c, the control group exhibited the most pronounced increase in conductivity, indicating the most severe membrane damage. The heat-treated group demonstrated a relatively high initial conductivity due to transient membrane damage induced by heat shock. However, its subsequent increase was less pronounced than that observed in the control group. In contrast, the HHP-treated groups, particularly the 300 MPa group, exhibited overall lower conductivity and a more gradual upward trend, suggesting that moderate high hydrostatic pressure can effectively preserve cell membrane integrity and mitigate electrolyte leakage[36].

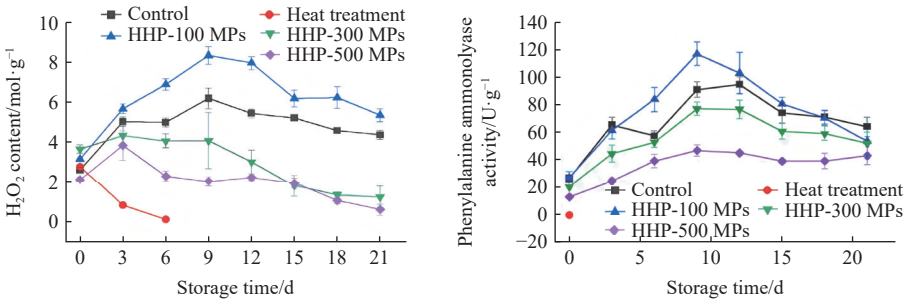
3.4.4 MDA content

Malondialdehyde (MDA), a key end product of membrane lipid

peroxidation, serves as an indicator of oxidative damage to plant cell membranes resulting from various treatments. As illustrated in Figure 5d, on the 0th day of storage, high-pressure treatments at 300 MPa and 500 MPa resulted in a significant increase in MDA content, rising by 123.80% and 80.95%, respectively, compared to the control group. This finding suggests that high pressure (≥300 MPa) inflicted immediate and severe physical damage to the cell membrane, thereby rapidly initiating the process of membrane lipid peroxidation. In contrast, no significant difference in MDA content was observed between the 100 MPa treatment, heat treatment, and the control group at this time (p>0.05). Throughout the subsequent storage period, each treatment group exhibited distinct dynamic patterns. The MDA levels in the control group continued to accumulate gradually, consistent with the natural aging process. Conversely, the MDA content in the heat treatment group initially increased sharply before subsequently decreasing. This phenomenon may result from the disintegration of the membrane structure induced by thermal shock, leading to significant lipid substrate leakage and rapid peroxidation. Additionally, the reaction rate diminished in the later stages as the substrate became depleted[37]. Notably, the accumulation rate of MDA in the 100 MPa treatment group was lower than that in the control group nine days prior to storage, but it subsequently exceeded that of the control group in the later stages. The treatment groups subjected to 300 MPa and 500 MPa consistently exhibited elevated levels of malondialdehyde (MDA), with the 300 MPa group demonstrating the most pronounced increase. This observation can be attributed to the damage mechanism of the membrane system induced by pressure, along with the resulting physiological responses[35]. The 300 MPa treatment led to a continuous and rapid accumulation of MDA, suggesting that this level of pressure elicited severe and sustained oxidative damage to the membranes[38].

3.4.5 Hydrogen peroxide (H_2O_2) content

Hydrogen peroxide (H_2O_2), a crucial reactive oxygen species signaling molecule, exhibits content changes that directly reflect the response intensity of plants to various stresses[39]. As shown in Figure 6a, HHP treatment resulted in significant H_2O_2 accumulation, with the effect being pressure-dependent. Conversely, heat treatment did not elicit a similar response. Initially, heat treatment did not alter the H_2O_2 level. Both the 100 MPa and 300 MPa treatments reached peak H_2O_2 content on the ninth day, approximately 2.6 times and 2.5 times the initial value, respectively. Notably, the H_2O_2 levels in the 100 MPa treatment group remained consistently higher than those in the other groups throughout the storage period. In contrast, the 500 MPa treatment resulted in a decrease in H_2O_2 content, maintaining it at a low level. These variations can be attributed to the differences in stress signals and cellular states.



a. H_2O_2 content b. Phenylalanine ammonolyase

Figure 6 Changes in H_2O_2 (a) and Phenylanine ammonolyase activity (b) of *Cistanche deserticola* slices caused by different treatment

The increase in H_2O_2 observed following treatments at 100 MPa and 300 MPa suggests that cells recognize stress as a responsive stress, thereby activating oxidative bursts that generate signaling molecules. This finding aligns with the research of Ortega et al., which indicates that abiotic stress can stimulate the production of reactive oxygen species, subsequently initiating defense responses, including the biosynthesis of phenolic compounds[40]. Notably, the consistently elevated levels of H_2O_2 during the 100 MPa treatment imply that this pressure induces a sustained active stress response state, serving as a critical REDOX signal driver for downstream defense metabolites, such as the activation of PAL and the early rapid accumulation of phenylethanol glycosides.

In contrast, the low concentration of H_2O_2 observed following treatment at 500 MPa likely indicates that the pressure intensity has surpassed the cell's tolerance threshold. This surpassing leads to disintegration of the cellular structure and a loss of metabolic function, thereby preventing the initiation of the normal stress signaling program. Consequently, the cells may enter a state of death or near death[41].

3.4.6 Activity of phenylalanine ammonia-lyase (PAL)

PAL serves as a crucial rate-limiting enzyme in the phenylpropane metabolic pathway, directly influencing the biosynthesis of phenolic compounds, including phenylethanol glycosides. As illustrated in Figure 6b, with the exception of complete PAL inactivation resulting from heat treatment, the activities of the other treatment groups exhibited a trend of initial increase followed by a decline, peaking around the 9th day of storage. Notably, the activity in the 100 MPa treatment group consistently paralleled that of the control group, maintaining a high level. In contrast, treatments at 300 MPa and 500 MPa significantly suppressed PAL activity (p<0.05). Importantly, the timing of peak PAL activity closely aligns with the peak in H_2O_2 content, suggesting a strong correlation between the two in signal transduction. This observation can be attributed to the signaling role of H_2O_2 and the direct impact of pressure on enzyme structure. H_2O_2, recognized as a key reactive oxygen species signaling molecule, can activate PAL expression at the transcriptional level, thereby facilitating phenylpropane metabolism[42].

The findings of this study align with several prior reports, which demonstrated that treatment with 50-100 MPa induces the production of reactive oxygen species in grape cells and significantly enhances PAL activity after 24 h[43]. Similarly, Viacava et al. reported a comparable trend in carrots, where treatments of 60 MPa and 100 MPa increased peak PAL activity by 380.2% and 139.7%, respectively, relative to the control[44]. Collectively, these

results suggest that moderate stress, such as 100 MPa, activates oxidative stress signals without compromising the protein structure and function of PAL, thereby effectively promoting the enzyme's activity and downstream secondary metabolism. In contrast, when pressure exceeds 300 MPa, PAL activity is markedly inhibited. This inhibition is not attributable to insufficient H_2O_2 signaling, as peak H_2O_2 levels remained relatively high in the 300 MPa group; rather, it is likely due to the direct disruption of the enzyme's protein conformation by elevated pressure[45]. Similar studies have demonstrated that enzymes, including polyphenol oxidase, experience irreversible denaturation and inactivation at pressures exceeding 400 MPa[46]. Furthermore, excessive pressure can result in overall metabolic disorders and energy depletion within cells, thereby impeding the synthesis and functional maintenance of phenylalanine ammonia-lyase (PAL).

3.5 Extraction yield of phenylethanol glycosides

As illustrated in Figure 7, extraction yield of phenylethanol glycosides was notably affected by the processing method and storage duration. Heat treatment resulted in a gradual reduction in phenylethanol glycoside content over the storage period. Conversely, HHP treatment generally improved the extraction yield of phenylethanol glycosides, with the impact variation based on pressure and duration. Specifically, at 100 MPa, the extraction yield peaked by day 9, surpassing the control group. Meanwhile, treatments at 300 MPa achieved maximum values on day 12. This indicates that moderate pressure (100 MPa and 300 MPa) facilitates early glycoside release, while higher pressures might delay extraction due to increased tissue compaction or altered physiological responses. The subsequent decline in yield post-peak suggests potential hydrolysis or degradation during prolonged storage. Remarkably, the 500 MPa treatment exhibited a more gradual decrease after reaching the peak, suggesting that extreme pressure could inhibit metabolic activity and decelerate the degradation of secondary metabolitesa[47], provides indirect evidence that the phenolic substances in this sample group may have undergone intense oxidative transformation, which is consistent with the results of Figure3f.

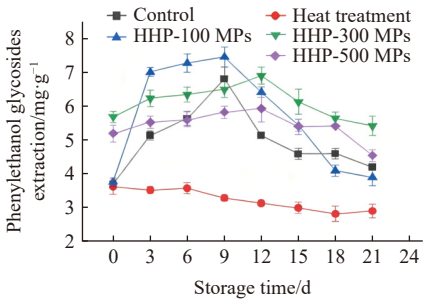


Figure 7 Changes in phenylethanol glycoside extraction of *Cistanche deserticola* slices caused by different treatment

To further investigate compositional changes, liquid chromatography-mass spectrometry was employed to compare phenylethanol glycoside profiles between HHP-treated and control samples, with heat-treated samples excluded due to low content. Among the 61 characterized compounds, most phenylethanol glycosides, including acteoside, Jionoside D, and Cistanoside C, exhibited up-regulation in HHP-treated groups compared to the control. Of the ten most abundant compounds, nine showed greater enrichment under HHP treatment, except for Cistanoside F. These results align with previous studies indicating that HHP enhances the retention and extraction of phenolic compounds in plant materials by disrupting cell walls and improving solvent accessibility[48]. The abundance of specific phenylethanol glycoside varied with pressure level and storage duration. Acteoside, Jionoside D, and Cistanoside C were more abundant after longer storage at 100 MPa, while Cistanoside E isomers (1) and (2) were more prevalent during shorter storage periods. Epimeridinoside A and Cistanoside D maintained consistent levels across all treatments. These changes highlight the influence of HHP on the extractability and stability of various phenylethanol glycosides during storage.

4 Conclusions

This study demonstrates that the impact of high hydrostatic pressure on fresh-cut *Cistanche deserticola* is significantly influenced by the applied pressure, resulting in two distinct processing strategies. For optimal quality preservation, treatment at 300 MPa is most effective, as it markedly inhibits microbial growth, minimizes weight loss, maintains color, and extends shelf life to 15 days. Conversely, while treatment at 500 MPa also exhibits a strong antibacterial effect, it leads to noticeable color deterioration during subsequent storage. Regarding the accumulation of bioactive compounds, the 100 MPa treatment stimulates the oxidative stress response, enhances the activity of phenylalanine ammonia-lyase (PAL), and facilitates the rapid synthesis of phenylethanol glycosides, peaking on the 9th day with a 34.17% increase compared to the control. Meanwhile, the 300 MPa treatment moderately suppresses basal metabolic activity and promotes the gradual and stable accumulation of glycosides. In conclusion, these findings suggest that high hydrostatic pressure can be precisely regulated through pressure selection, thereby facilitating either a rapid increase in bioactive content or balanced quality preservation, thus offering a targeted non-thermal processing method for enhancing the quality and value of medicinal food plants.

Acknowledgements

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