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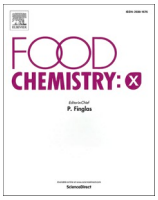

Dicyclohexylcarbodiimide and disodium succinate induce the change of energy metabolism in relation to longan pulp breakdown

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ABSTRACT

Compared to control longan, DCC-treated longan had higher pulp breakdown index, lower ATP, ADP and EC levels, and lower H^+, Ca^{2+} and Mg^{2+}-ATPase activities. On day 6, DCC-treated longan presented 18% higher pulp breakdown index, with 44%, 9% and 31% lower levels of ATP, ADP and EC, respectively. Additionally, DCC-treated longan showed 29%, 53%, 37% lower activity of H^+-ATPase, 34%, 54%, 4% lower activity of Ca^{2+}-ATPase, and 13%, 21%, 6% lower activity of Mg^{2+}-ATPase in the membranes of plasma, vacuole, and mitochondria, respectively. Whereas, DS-treated longan manifested the opposite trends of DCC treatment. These results suggest that the accelerated pulp breakdown in DCC-treated longan was linked to energy deficiency and reduced energy production. However, DS treatment restrained pulp breakdown occurrence in fresh longan by maintaining a higher energy level through the elevated energy production and ATPase activity.

1. Introduction

Longan (*Dimocarpus longan* Lour.) is a significant subtropical specialty fruit in southern China, highly valued for its unique flavor, rich nutrition, and beneficial bioactive components that promote human health (Zeng, Wang, Liu, Hu, & Zhao, 2024). Nevertheless, longan fruit ripens during the seasons with high humidity and temperature, leading to vigorous metabolic activities and a rapid decline in quality after harvest (Lin, Lin, Lin, Chen et al., 2023). Pulp breakdown is the main problem that leads to quality decline in postharvest longan, manifested as pulp softening, juice-oozing, and spoilage (Lin et al., 2019; Lin et al., 2020; Liu et al., 2022; Sun et al., 2022). This not only influences the quality attributes of longan, but also diminishes its market value and shelf life. Thus, it is urgent to enunciate the mechanism of longan pulp breakdown and develop its control technologies.

Energy status, a key determinant of the quality in fresh produces, is regulated by the pathway of energy metabolism. The basis of energy metabolism involves adenosine triphosphate (ATP) and its catabolic products, including adenosine diphosphate (ADP) and adenosine monophosphate (AMP), and the relationship among which can be expressed in energy charge (EC) (Lin et al., 2017a). Moreover, prior works suggested that the deterioration in fresh produce was related to physiological disorder under various adverse conditions. The adverse conditions can damage the structure and function of cellular membranes and cellular organelles (involving mitochondria, plasma, vacuole), finally leading to energy deficiency in plant cells (Lin et al., 2020). Additionally, adenosine triphosphatase (ATPase) (including H^+, Ca^{2+}, and Mg^{2+}-ATPase) are located in the mitochondrial membranes (MM), plasma membranes (PM), and vacuolar membranes (VM), playing a crucial role in energy metabolism to ensure the normal operation of physiological and biochemical processes within cells (Lin et al., 2020). For plant tissues, an adequate energy supply is vital for the proper functioning of many physiological metabolisms. The activation of energy metabolism effectively enhances the fruit storability including

Abbreviations: ADP, adenosine diphosphate; AMP, adenosine monophosphate; ATP, adenosine triphosphate; ATPase, adenosine triphosphatase; DCC, dicyclohexylcarbodiimide; DS, disodium succinate; EDTA, ethylene diamine tetraacetic acid; EC, energy charge; $HClO_4$, perchloric acid; KOH, potassium hydroxide; M, mol L^{-1}; mM, mmol L^{-1}; MM, mitochondrial membrane; PM, plasma membrane; VM, vacuolar membrane.

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mango (Huang et al., 2024), papaya (Zhou et al., 2024) and fig. (Wang, Jing et al., 2024). Conversely, the reduced efficiency of energy production and the inadequate supply of energy are often associated with the senescence and physiological disorders in fresh produces (Wang, Jing, et al., 2024).

Dicyclohexylcarbodiimide (DCC) can block ATP synthesis, thereby reducing energy production and leading to energy deficiency (Blbulyan & Trchounian, 2015; Toei & Noji, 2013). On the contrary, disodium succinate (DS) can enhance the synthesis of ATP, and thus maintain a higher energy level (Sun, Bai, Li, & Guo, 2019).Our work has shown that DCC and DS treatment could adjust the process of quality decline in fresh longan like longan pericarp browning (Chen et al., 2023; Lin et al., 2024) and longan pulp breakdown (Zheng et al., 2024). Whereas, the impacts of DCC and DS on the energy state and their relationship with the development of longan pulp breakdown are still unclear. Hence, the objective of this work is to explore the effects of DCC and DS on the energy state and the breakdown development of longan pulp, so as to enunciate the mechanism of longan pulp breakdown. Our findings can offer new insights into the mechanism of longan pulp breakdown and present new strategies to slow down the development of longan pulp breakdown, thereby sustaining the quality attributes and extending the shelf life of postharvest longans.

2. Materials and methods

2.1. Reagents

DCC, DS, benzyl sulfonyl chloride, and sodium vanadate were obtained from Macklin Biochemical (Shanghai, China). Perchloric acid ($HClO_4$) was acquired from Beijing Chemical Industry Group (Beijing, China). Potassium hydroxide (KOH), hydrochloric acid, potassium dihydrogen phosphate, dipotassium hydrogenphosphate, ethylene diamine tetraacetic acid (EDTA), glycerol, vitamin C, sucrose, trichloroacetic acid, magnesium sulphate, potassium chloride, sodium chloride, calcium chloride, magnesium chloride, sodium azide, and potassium nitrate were acquired from Sinopharm Chemical Reagent (Shanghai, China). Dithiothreitol and Tris were obtained from Solarbio Science & Technology (Beijing, China). The above reagents used in this study were analytical grade.

Methanol (Chromatographic purity) was purchased from Merck KGaA (Darmstadt, Germany). ATP, ADP, and AMP (Chromatographic purity) were acquired from Yingxin laboratory equipment (Shanghai, China).

2.2. Longan fruit and treatment

'Fuyan' longan fruits, at commercial maturity with a light yellowish-brown of longan fruit appearance, 15.43% ± 0.38% of total soluble solid content and 0.050% ± 0.003% of titratable acid content in longan pulp, were harvested from Nan'an orchard, Fujian, China. The harvested longan fruits were pre-cooled at 3–4 °C for 3 h, then the fruits were transported to our lab in Fuzhou by using a refrigerated truck at 8 °C. Fruits of defect-free and uniform size were chosen and rinsed with deionized water. Following the wash, 300 fruits were chosen for trait analysis on the day of harvest, while the rest were divided into three batches, each comprising 1800 fruits. The first batch served as the control group and was soaked for 15 min with distilled water, while the other two batches were treated, being soaked in solutions of 40 mM DS and 0.4 mM DCC, respectively, for 15 min each. The concentrations of DS and DCC used in this study were cited our prior study (Chen et al., 2023). After treatment, the fruits were air-dried and packaged in polyethylene film bag (36 bags per treatment and 50 longans per bag), then kept at 25 °C and 85% relative humidity. Within the storage duration, six bags of longan (300 fruits) were taken from each group every day to monitor the breakdown process of longan pulp, and the longan pulps were ground using liquid nitrogen to acquire longan pulp powder, then the longan pulp powder was kept at −80 °C for measuring the subsequent metrics.

2.3. Assessment of longan pulp breakdown

Referring to the detail approach described by our prior study (Chen et al., 2015), pulp breakdown was assessed by measuring the extent of the total breakdown area in pulp of 50 individual longan fruits using the following visual appearance classes: 0, no breakdown; 1, breakdown area $< 1/4$; 2, $1/4 \leq$ breakdown area $< 1/2$; 3, $1/2 \leq$ breakdown area $< 3/4$; 4, breakdown area $\geq 3/4$. The calculation formula $\sum$ (breakdown class × proportions of corresponding longans in each class) was used to calculate the pulp breakdown index.

2.4. Quantification of adenine nucleotides and EC level

The level of EC, ATP, ADP, and AMP were estimated following the approach of Lin et al. (2024) with a slight modification. Frozen powder of longan pulp (10 g) was dissolved with 600 mM $HClO_4$ and centrifuged for obtaining the supernatants. Thereafter, the pH value of the supernatants was regulated to 6.5–6.8 using 1 M KOH, then the supernatants were filtered with a filter (0.45 μm) for subsequent test. The test solution was evaluated the adenine nucleotides (AMP, ADP, ATP) contents by HPLC-2030C (Shimadzu, Japan) with a Waters XBridge C18 column. The units of adenine nucleotides were denoted in mg kg^{-1}.

The calculation formula [ATP + 1/2 ADP] / [AMP + ADP + ATP] was applied for calculating the EC level based on the above-measured contents of adenine nucleotides.

2.5. ATPase activity

The extraction and activity analyses of ATPase (H^+, Mg^{2+}, and Ca^{2+}-ATPase) in PM, MM, and VM were conducted based on the approach of our prior study (Lin et al., 2017b) with some modifications. Frozen powder of longan pulp (5 g) was dissolved with the extraction medium, which included EDTA (5 mM), dithiothreitol (5 mM), benzyl sulfonyl chloride (1 mM), glycerol (5%), vitamin C (10 mM), sucrose (250 mM) and Tris (80 mM), and centrifuged to obtain the supernatants as the enzyme solution for subsequent assays. Depending on the type of ATPase, the corresponding reaction solution, ATP (5 mM), and the enzyme solution were mixed, then incubated for 10 min at 36 °C. After incubation, 20% (*w/v*) trichloroacetic acid was added to the reaction mixture solution for terminating the reaction, and the obtained reaction solution was centrifuged. Subsequently, the obtained supernatant was added to reaction solution (including ferrous sulfate-ammonium molybdate reagent and distilled water), then the absorbance of above reaction mixture solution was detected at 660 nm.

Protein quantitative analyses of above ATPase enzyme solution were performed referring to the approach of Bradford (1976), and U kg^{-1} protein was adopted for denoting the unit of ATPase activity.

2.6. Statistical analysis

All metrics were measured in triplicate. The data in all figures were displayed as the means ± standard errors ($n = 3$). The acquired data were analyzed using IBM SPSS version 22.0. The symbol * or ** (DCC-treated longan), and * or ** (DS-treated longan) in the figures separately indicated significant differences ($P < 0.05$) or extremely significant differences ($P < 0.01$) when compared with the control longan on the same storage day. In addition, the correlations between the metrics were analyzed using Pearson correlation test, and R package ggcorrplot was applied to draw the correlation heatmap.

3. Results

3.1. The appearance and breakdown index in longan pulp

At day 0, longan pulp was observed to be white, translucent, and plump (Fig. 1A). After six days of storage, the control longan displayed significant flesh breakdown, characterized by a loss of white color, translucency, and initially intact appearance of the pulp (Fig. 1B). Additionally, the DCC treatment remarkably accelerated the breakdown process in the longan pulp, leading to browning and significant damage to the pulp appearance (Fig. 1C). Compared to the control longan, DCC-treated longans showed a higher pulp breakdown index, demonstrating a clear increase between days 2 and 6 (Fig. 1E). However, DS treatment effectively delayed the breakdown process in the longan pulp (Fig. 1D), with a clearly lower pulp breakdown index observed in DS-treated longan than the control longan from days 2 to 5 (Fig. 1E). On day 6, 18% higher level and 11% lower level of pulp breakdown index were separately displayed in DCC-treated longan and DS-treated longan than the control longan.

The above data suggest that DCC treatment could accelerate the breakdown process in longan pulp, whereas DS treatment could slow down the breakdown process in the longan pulp.

3.2. The EC, ATP, ADP, and AMP levels

Fig. 2A–2C illustrate that the values of EC, ATP, and ADP in all three groups significantly and continuously decreased during storage. On day 6, the levels of ATP, ADP and EC in DCC-treated longan were 44%, 9%, and 31% lower than those in the control longan, respectively. However, DS treatment delayed these declines and exhibited higher values of ATP, ADP, and EC than those in the control longan during storage. For example, on day 6, the values of ATP, ADP, and EC in DS-treated longan were 34%, 16% and 22% higher than those in the control longan, separately.

AMP content showed an increasing trend in all three groups as storage time extended (Fig. 2D). Compared to the control longan, DCC treatment accelerated an increment in AMP content, while DS treatment moderated it. For example, on day 6, DCC-treated longan presented 26% higher AMP amount, whereas DS-treated longan showed 9% lower level of AMP as compared with the control longan.

The above data suggest that DCC-treated longan showed the accelerated declines of pulp EC, ATP, and ADP levels, along with an enhanced accumulation of AMP. Conversely, DS-treated longan exhibited a decelerated process in these biochemical changes.

3.3. ATPase activity

Fig. 3A–3C illustrate that, for the control longan, H^+-ATPase activity of PM increased from days 0 to 1, while H^+-ATPase activity of VM and MM enhanced from days 0 to 2. Subsequently, H^+-ATPase activity in all three groups decreased continuously until day 6. Compared to the control longan, DCC treatment clearly reduced H^+-ATPase level, but DS treatment promoted H^+-ATPase activity throughout the whole storage duration. For example, on day 6, DCC-treated longan presented 29%, 53%, and 37% lower activity of H^+-ATPase in PM, VM and MM, separately, whereas, 16%, 23%, and 16% higher levels of those indices were shown in DS-treated longan, respectively, as compared to the control longan.

Fig. 3D–3F suggest that Ca^{2+}-ATPase activity in the control longan fluctuated slightly before two storage days, and gradually decreased during days 2–6. Compared with the control longan, DCC treatment decreased the Ca^{2+}-ATPase activity, but DS treatment elevated Ca^{2+}-ATPase activity within the storage. For example, on day 6, compared to the control longan, the activities of Ca^{2+}-ATPase in PM, VM and MM of DCC-treated longan were reduced by 34%, 54%, and 4%, respectively, whereas those indices in DS-treated longan were elevated by 67%, 60%, and 7%, separately.

For the control longan, Mg^{2+}-ATPase activity in PM continued to decline within storage, while Mg^{2+}-ATPase activity in VM and MM were increased during days 0–2, and then fell from days 2 to 6 (Fig. 3G–3I). Compared to the control longan, DCC treatment reduced the Mg^{2+}-ATPase activity, but DS treatment elevated the Mg^{2+}-ATPase activity within storage. For example, on day 6, the levels of Mg^{2+}-ATPase in PM, VM and MM of DCC-treated longan were 13%, 21%, 6% lower than those in the control longan, respectively, whereas those indices in DS-treated longan were elevated by 11%, 15%, and 11% than the control longan, separately.

The above results indicate that DCC treatment could lower activity of H^+, Ca^{2+}, and Mg^{2+}-ATPase in PM, VM and MM of longan pulp, however, DS treatment could retain higher levels of those indices in pulp of longan fruit during storage.

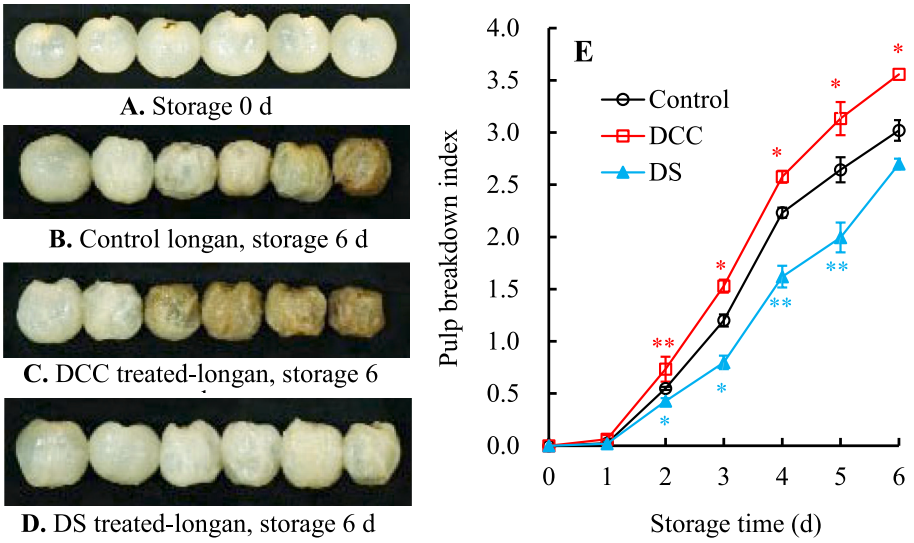

Fig. 1. The impacts of DCC and DS treatments on the pulp appearance (A–D) and the pulp breakdown index (E) in longan fruit during storage. Each data is the mean ± standard error of three repetitions. The symbol * or ** (DCC-treated longan), and * or ** (DS-treated longan) in the figures separately indicated significant differences ($P < 0.05$) or extremely significant differences ($P < 0.01$) when compared with the control longan on the same storage day. ○, Control; □, 0.4 mM DCC; ▲, 40 mM DS. DCC, dicyclohexylcarbodiimide; DS, disodium succinate. The pulp breakdown index (Fig. 1E) was quoted from our work published in *Postharvest Biology and Technology* by Zheng et al. (2024) (https://doi.org/10.1016/j.postharvbio.2024.113041).

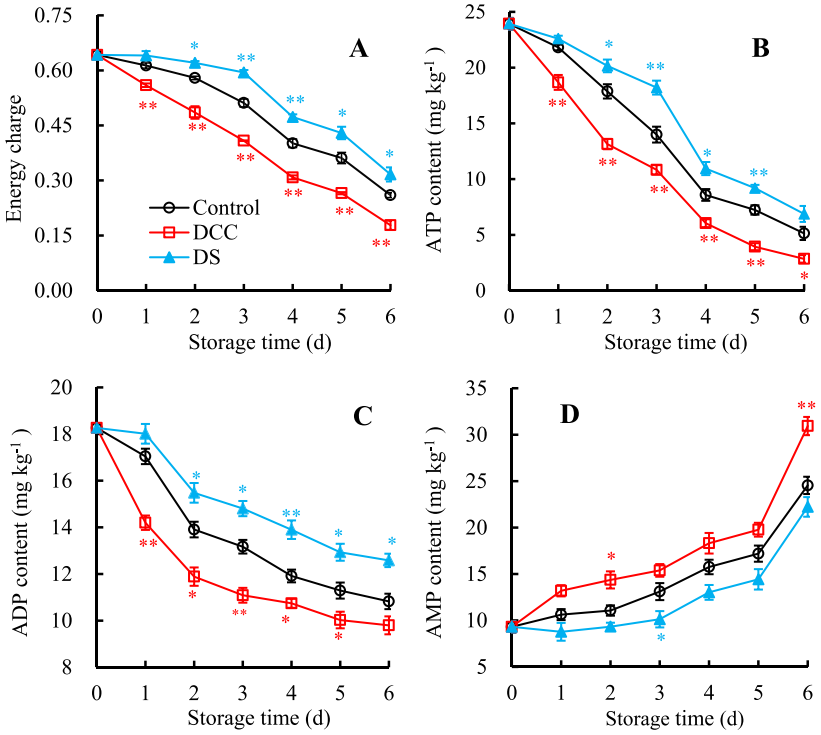

Fig. 2. The impacts of DCC and DS treatments on the energy charge (A) and the amounts of ATP (B), ADP (C) and AMP (D) in pulp of longan fruit during storage. Each data is the mean ± standard error of three repetitions. The symbol * or ** (DCC-treated longan), and * or ** (DS-treated longan) in the figures separately indicated significant differences ($P < 0.05$) or extremely significant differences ($P < 0.01$) when compared with the control longan on the same storage day. ○, Control; □, 0.4 mM DCC; ▲, 40 mM DS. DCC, dicyclohexylcarbodiimide; DS, disodium succinate; ATP, adenosine triphosphate; ADP, adenosine diphosphate; AMP, adenosine monophosphate.

4. Discussion

4.1. DCC and DS regulated longan pulp breakdown by influencing energy status

Energy state takes a vital role in the maturation and senescence of fresh product (Lin, Lin, Lin, Lin et al., 2023). ATP, ADP, and AMP are three major energy metabolizers that affect the cellular energy status. Among them, ATP is the direct substance of energy involved in the metabolic activity of cell (Liu et al., 2023). EC serves as a quantitative parameter for the relationship between ATP, ADP, and AMP, reflecting the energy reserves in plant cells. The relationship between energy levels and quality decline in postharvest produce has been demonstrated through experiments with ATP treatment, confirming that a high energy level in fresh produce could maintain structural integrity and function of mitochondria, thus effectively delaying spoilage in pears (Duan et al., 2019), mung beans (Chen et al., 2019), and strawberries (Li et al., 2021). However, energy depletion, induced by 2,4-dinitrophenol treatment, could reduce stress resistance, and exacerbate physiological disorders in strawberries and apples (Guo, Liu, Bai, Yan, & Li, 2018; Shu, Cao, & Jiang, 2022).

Within the storage, as the pulp breakdown index (Fig. 1E) in all treated-longans gradually rose, the values of EC (Fig. 2A), ATP (Fig. 2B), and ADP (Fig. 2C) decreased, but the AMP content (Fig. 2D) increased. For three treatment groups, correlation analyses discovered that the pulp breakdown index had negative correlations with the values of EC, ATP, and ADP, but positive correlation with AMP amount (Fig. 4). This suggests that the breakdown occurrence of longan pulp connected with the decreasing values of EC, ATP, and ADP, as well as with an increasing AMP amount. Furthermore, the AMP content was negatively correlated with ADP and ATP levels, indicating that AMP synthesis related to the consumptions of ADP and ATP (Fig. 4). These data suggest that the breakdown occurrence of longan pulp was associated with ADP and ATP degradations, and AMP production.

Furthermore, compared to the control longan, DCC-treated longan manifested higher pulp breakdown index (Fig. 1E) and AMP amount (Fig. 2D), but lower values of EC (Fig. 2A), ATP (Fig. 2B), and ADP (Fig. 2C) during storage. It suggests that DCC treatment exacerbated the breakdown occurrence of longan pulp, which was due to the decreased EC, ADP and ATP values, and a quick increment in AMP content. On the contrary, the DS-treated longan displayed higher contents of energy levels (EC, ATP, ADP) (Fig. 2A, B, C) but lower AMP level (Fig. 2D), indicating that DS treatment postponed the breakdown occurrence of longan pulp by decreasing EC level, manifested as ADP and ATP degradations, and AMP production.

4.2. DCC and DS regulated longan pulp breakdown by affecting ATPase activity

Energy status is strongly linked to the variation of ATPase activity. ATPase, a class of transmembrane proteases, is mainly distributed in PM, MM, and VM, including H^+, Ca^{2+} and Mg^{2+}-ATPase. It affects the stability of the normal energy metabolism and intracellular environment, and is involved in information transfer, material transport and energy conversion (Falhof, Pedersen, Fuglsang, & Palmgren, 2016; Lin et al., 2024). H^+-ATPase is linked to the formation and availability of energy substance (Jia, Liu, & He, 2024). As ionic regulators, Ca^{2+} and Mg^{2+}-ATPase can transfer the corresponding ions from the cytoplasm to extracellular or organelles, helping to balance the intracellular and extracellular ionic environment and maintain cell membrane integrity (Lin et al., 2020). Guan, Fan, Dou, Zhang, and Li (2006) found that peach fruit senescence was closely connected with the activity of Ca^{2+}-ATPase. Moreover, it was suggested that the decay of apple fruit was caused by the fallen levels in H^+ and Ca^{2+}-ATPase, so as to reduce the

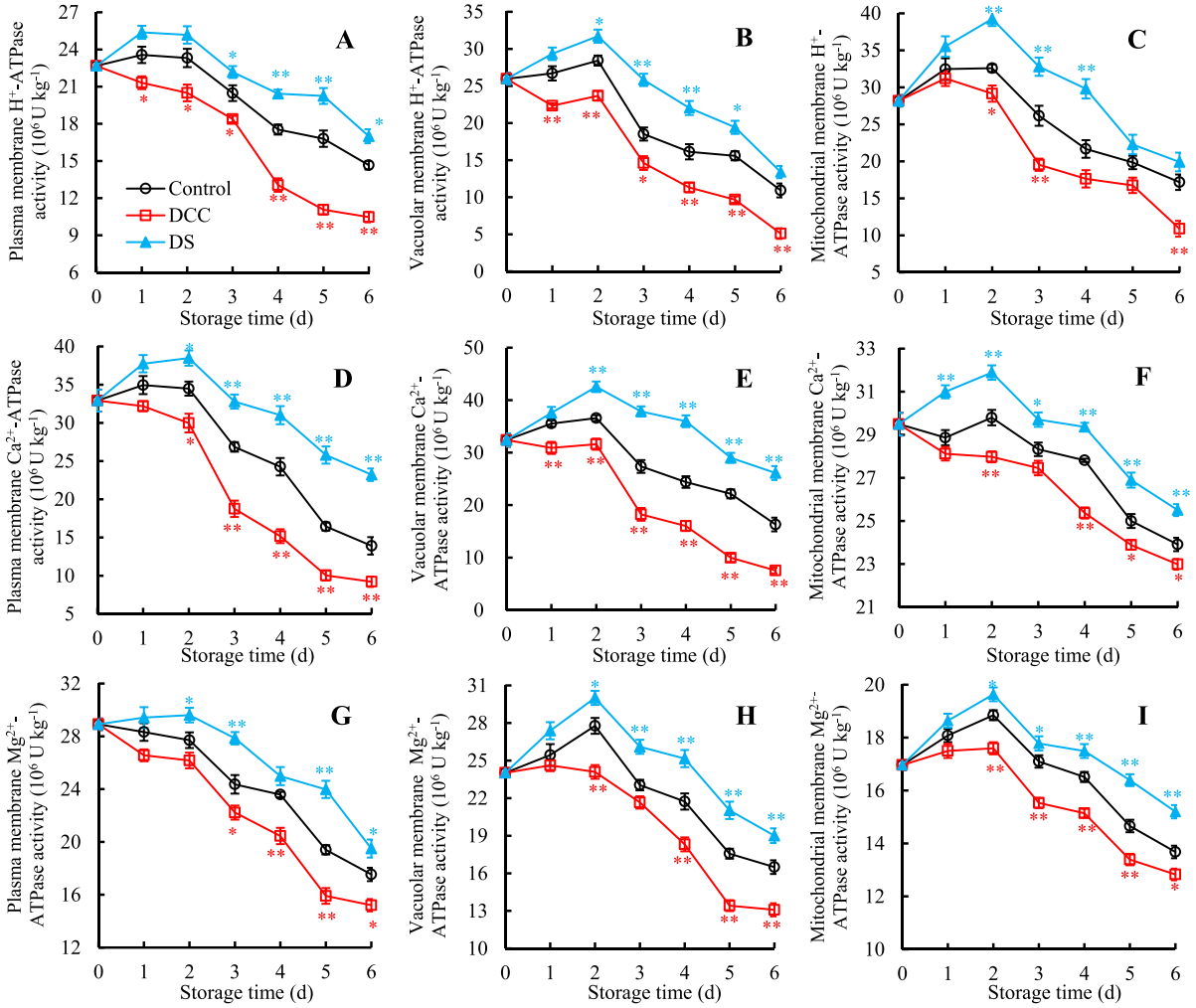

Fig. 3. The impacts of DCC and DS treatments on the ATPase activity in pulp of longan fruit during storage. H^+-ATPase in the membranes of plasma, vacuole, and mitochondria (A–C), Ca^{2+}-ATPase in the membranes of plasma, vacuole, and mitochondria (D–F), and Mg^{2+}-ATPase in the membranes of plasma, vacuole, and mitochondria (G–I). The symbol * or ** (DCC-treated longan), and * or ** (DS-treated longan) in the figures separately indicated significant differences ($P < 0.05$) or extremely significant differences ($P < 0.01$) when compared with the control longan on the same storage day. ○, Control; □, 0.4 mM DCC; ▲, 40 mM DS. DCC, dicyclohexylcarbodiimide; DS, disodium succinate; ATPase, adenosine triphosphatase.

ATP, ADP, and EC values (Wang, Li et al., 2024). Whereas, some studies showed that maintaining cellular osmotic pressure and energy levels by increasing ATPase activity could delay spoilage in apples (Li et al., 2020) and litchis (Zhang et al., 2021).

Within the storage, as the pulp breakdown index (Fig. 1E) in all treated-longans gradually rose, the values of EC (Fig. 2A), ATP (Fig. 2B), and ADP (Fig. 2C) decreased, but the AMP content increased (Fig. 2D). In addition, H^+, Ca^{2+} and Mg^{2+}-ATPase activity in these treated samples generally followed a pattern of initial increase and then decrease (Fig. 3A–3I). For three treatment groups, correlation analyses discovered that the pulp breakdown index had negative correlations with the values of ATPase (H^+, Ca^{2+}, Mg^{2+}-ATPase) (Fig. 4). This suggests that the breakdown occurrence of longan pulp connected with the decreasing ATPase activity. In addition, ATPase (H^+, Ca^{2+}, Mg^{2+}-ATPase) activity had positive correlations with EC, ATP, and ADP levels, but negative correlation with AMP content, implying that ATPase activity affected the content of energy metabolites in longan pulp (Fig. 4). These data suggest that the breakdown occurrence of longan pulp was associated with an inhibited ATPase activity, which possibly led to decreased ADP and ATP contents, and increased AMP level.

Compared with the control longan, throughout the storage, DCC-treated longan manifested higher pulp breakdown index (Fig. 1E) and AMP amount (Fig. 2D), but lower values of ATP (Fig. 2B), ADP (Fig. 2C), and ATPase (H^+, Ca^{2+}, Mg^{2+}-ATPase) (Fig. 3A–3I). It suggests that DCC treatment exacerbated the breakdown occurrence of longan pulp, which was due to an inhibited ATPase activity. This led to the quick declines in ADP and ATP values, and a quick increment in AMP content. On the contrary, the DS-treated longan showed higher ATPase (H^+, Ca^{2+}, Mg^{2+}-ATPase) activity (Fig. 3A–3I) and higher contents of energy metabolizing substances (ATP, ADP) (Fig. 2B, C), suggesting that DS treatment delayed the breakdown occurrence of longan pulp by maintaining higher ATPase activity to reduce ADP and ATP degradations, and AMP production.

5. Conclusions

In summary, this study revealed a close correlation between the energy metabolism and pulp breakdown occurrence of fresh longan. DCC-induced the accelerated longan pulp breakdown occurrence was due to DCC-reduced activities of ATPases (Ca^{2+}, Mg^{2+}, H^+-ATPase) in PM, MM, and VM, as well as a decrease in EC, ADP, and ATP levels. These results might lead to an imbalance in intracellular environment and changes in cellular properties and integrity, which in turn triggered metabolic disorders and damaged to cell membranes and organelles,

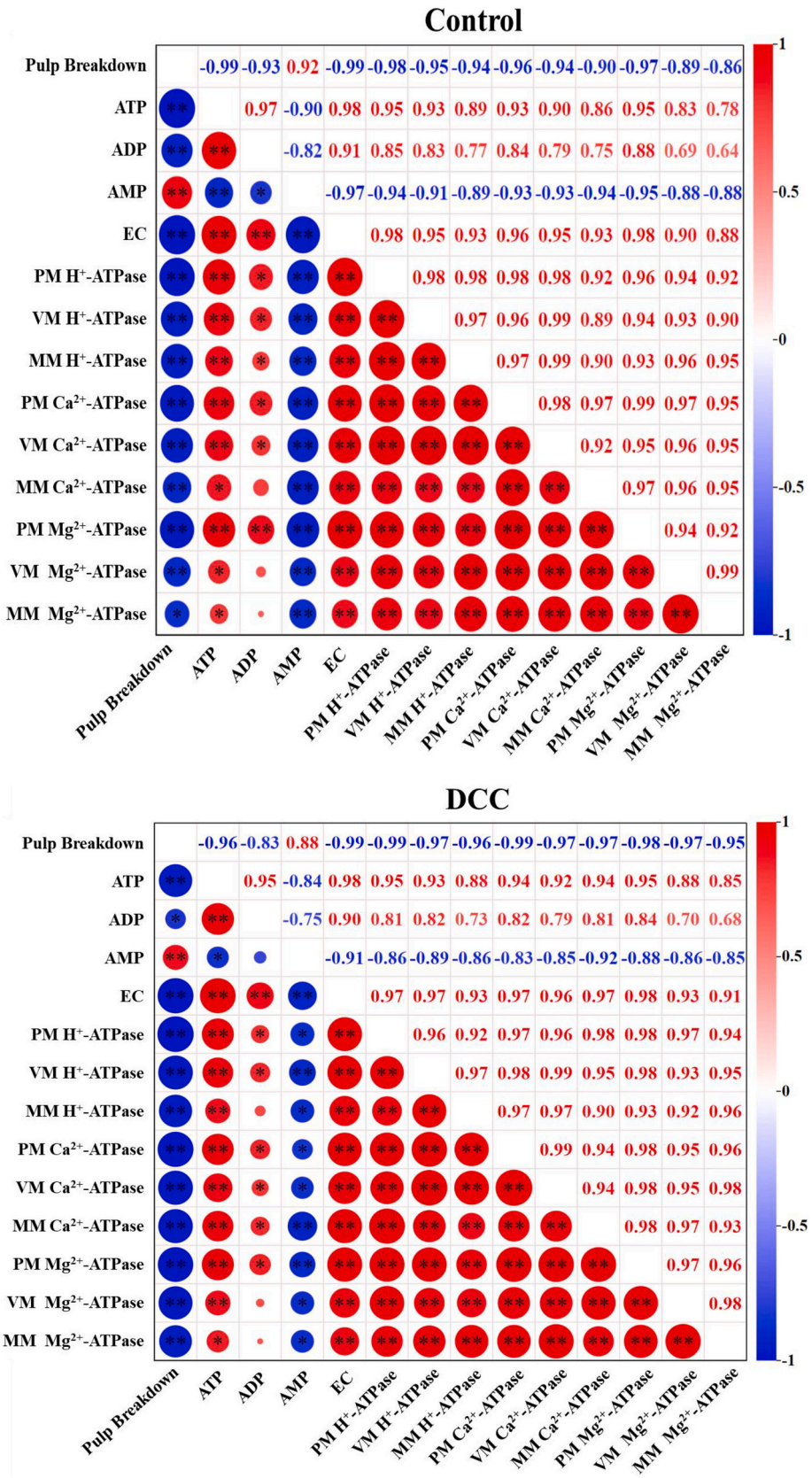

Fig. 4. Heatmap of Pearson's correlation analyses between the estimated metrics related to the pulp breakdown and the metabolism of energy in the control longan, DCC-treated longan, and DS-treated longan during storage (*$P < 0.05$, **$P < 0.01$). Red indicated a positive correlation, while blue indicated a negative correlation. DCC, dicyclohexylcarbodiimide; DS, disodium succinate; ATP, adenosine triphosphate; ADP, adenosine diphosphate; AMP, adenosine monophosphate; EC, energy charge; ATPase, adenosine triphosphatase; PM, plasma membrane; VM, vacuolar membrane; MM, mitochondrial membrane. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

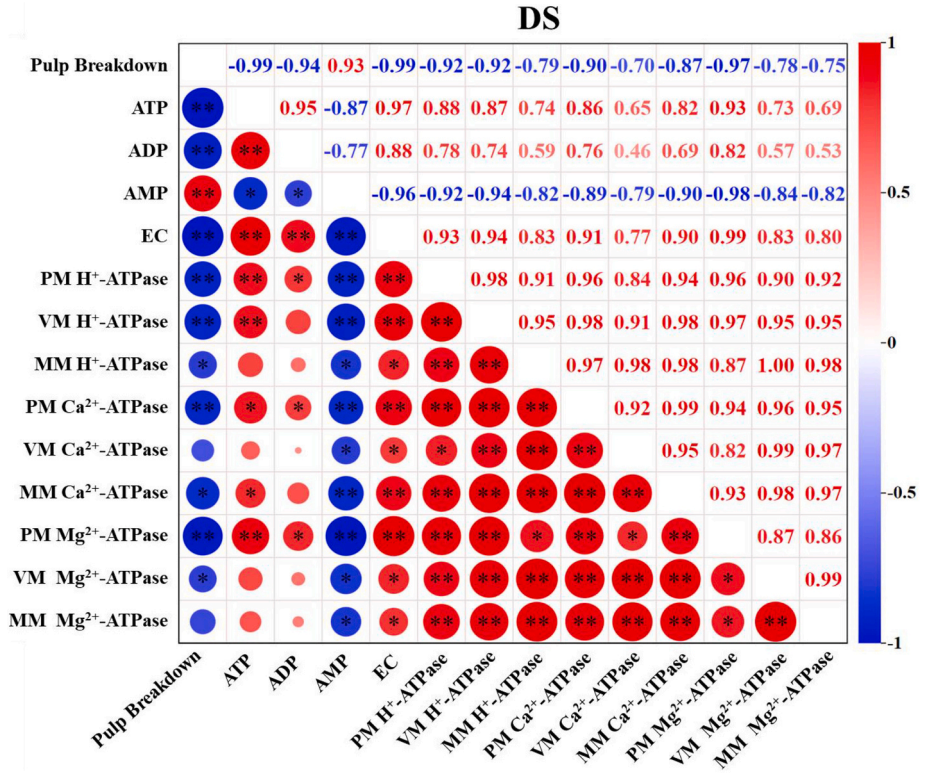

Fig. 4. (*continued*).

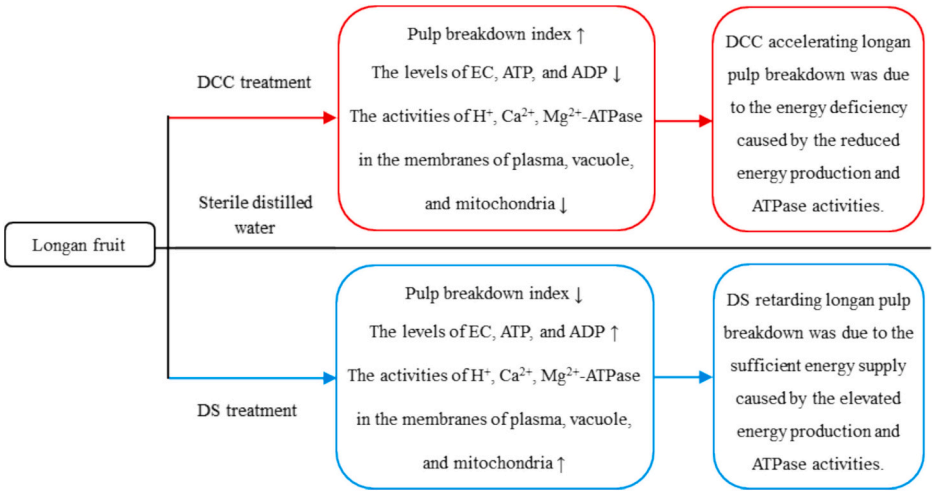

Fig. 5. The potential mechanisms of DCC and DS treatments regulating longan pulp breakdown via modulating energy metabolism. The up arrow (↑) in the figure indicated the higher levels of metrics in the DCC-treated longan or in the DS-treated longan when compared with the control longan; while the down arrow (↓) in the figure indicated the lower levels of metrics in the DCC-treated longan or in the DS-treated longan when compared with the control longan. DCC, dicyclohexylcarbodiimide; DS, disodium succinate; EC, energy charge; ATP, adenosine triphosphate; ADP, adenosine diphosphate; ATPase, adenosine triphosphatase.

thereby exacerbating the pulp breakdown occurrence of fresh longan. However, DS treatment helped to maintain ATPase activity and energy level, thus suppressing the onset of longan pulp breakdown. These data offer valuable insights of DCC and DS regulating longan pulp breakdown through adjusting energy metabolism, and their possible mechanisms were encapsulated in Fig. 5. Whereas, the molecular mechanism of DCC and DS regulating the breakdown development of longan pulp is still unclear. Consequently, the molecular mechanism of DCC and DS adjusting the breakdown occurrence of longan pulp needs further elucidation.

This study also suggests that DS treatment effectively suppressed the pulp breakdown of postharvest longan fruit. In addition, DS has the advantages of low price, chemical stability, and safety, and has been widely used in the food industry. This indicates that DS is a potential alternative approach for delaying the development of longan pulp breakdown and prolonging the storage-life of postharvest longan fruit.

CRediT authorship contribution statement

Yi Zheng: Writing – original draft, Investigation, Formal analysis, Data curation. **Hetong Lin:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Yueying Sang: Writing – original draft. **Mengshi Lin:** Writing – review & editing. **Yixiong Lin:** Project administration, Investigation. **Hui Wang:** Investigation. **Zhongqi Fan:** Investigation. **Yihui Chen:** Investigation. **Yifen Lin:** Writing – review & editing, Project administration, Funding acquisition.

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

The authors do not have permission to share data.

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