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Short communication

Hydrogen peroxide-induced pericarp browning of harvested longan fruit in association with energy metabolism

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ABSTRACT

Energy metabolism of "Fuyan" longan fruit treated with hydrogen peroxide (H_2O_2), the most stable of the reactive oxygen, and its relationship to pericarp browning were investigated in this work. The results displayed that H_2O_2 significantly decreased contents of adenosine triphosphate (ATP) and adenosine diphosphate (ADP). It also inhibited activities of H^+-ATPase, Ca^{2+}-ATPase and Mg^{2+}-ATPase in membranes of plasma, vacuole and mitochondria during the early-storage and mid-storage (except for mitochondrial membrane Mg^{2+}-ATPase). These results gave convincing evidence that the treatment of H_2O_2 accelerating pericarp browning in harvested longans was due to a decrease of ATPase activity and available ATP content. This might break the ion homeostasis and the integrity of mitochondria, which might reduce energy charge and destroy the function and compartmentalization of cell membrane. These together aggravated browning incidence in pericarp of harvested longan fruit.

1. Introduction

Longan (*Dimocarpus longan* Lour.) fruit is globally consumed with high commercial value. However, pericarp browning is one of the common problems in longan industry (Jiang, Zhang, Joyce, & Ketsa, 2002; Lin et al., 2017). Browning occurrence should be the result of the contact of phenolics and phenolase, which can be attributed to the loss of cellular compartmentalized distribution (Jiang et al., 2002; Lin, Lin, Lin et al., 2016; Yi et al., 2010). Accumulating evidence reveals that energy supply is closely associated with cell membrane function. The shortage in energy and adenosine triphosphate (ATP) may trigger the deterioration and decompartmentalization of biological membrane (Chumyam, Shank, Uthaibutra, & Saengnil, 2016; Jiang et al., 2007; Saquet, Streif, & Bangerth, 2003), while higher energy and ATP content may account for better maintenance of biological membrane structure as well as less susceptibility to browning (Chen et al., 2014, 2015; Jin, Zhu, Wang, Shan, & Zheng, 2014).

Mitochondrion, called as power house, takes the first place for respiration metabolism and the production of ATP, which provide energy for the normal activities (Olsen, Andersen, Lunding, Brasen, & Poulsen, 2009). Various of life activities are conducted in the environment surrounded by biological membrane. The transmembrane transport of all kinds of inorganic or organic ions is indispensable to life activities (Morsomme & Boutry, 2000). However, ions cannot transport freely across the membrane due to the hydrophobicity of lipid bilayer structure in biological membrane (Kasamo, 2003). Proton electrochemical potential gradient, established rely on the hydrolysis of ATP by adenosine triphosphatase (ATPase), is the driving force to transport all kinds of ions and small molecules (metabolites) across the biological membrane (Falhof, Pedersen, Fuglsang, & Palmgren, 2016). The conformation and function of ATPase is regulated by the fluidity of membranes. Decrease in the fluidity increases the proportion of membrane protein exposed to aqueous phase. The peroxidation of membrane lipid caused by abundant reactive oxygen species (ROS) is an important factor to reduce the fluidity of membrane, accordingly, to destruct the structure of phospholipid bilayer and change the conformation of ATPase (Gao, Yao, & Squier, 2001). Besides, almost all proteins or enzymes can be oxidative modified by ROS, whose accumulation may result in the reduction of ATPase activity (Yin, Kuczera, & Squier, 2000).

It is suggested that the low incidence of pitting or browning is associated with the enhancement in levels of ATP and energy as well as activities of mitochondrial H^+-ATPase and Ca^{2+}-ATPase, which can maintain mitochondrial structure and normal respira-

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tory metabolism (Li, Limwachiranon, Li, Du, & Luo, 2016; Liu et al., 2016). Our previous work showed that hydrogen peroxide (H_2O_2) could induce the production and accumulation of ROS, accelerating the degradation of cell membrane and browning in pericarp of harvested longan fruit (Lin et al., 2014, Lin, Lin, Lin et al. 2016). It also could change the pathway of respiratory metabolism and decrease the energy charge of harvested longan fruit (Lin, Lin, Chen et al., 2016).

Currently, no studies have been published on the role of energy metabolism in longan pericarp browning caused by H_2O_2. Therefore, in order to reveal their relation, the effects of H_2O_2 on contents of ATP, adenosine diphosphate (ADP) and adenosine monophosphate (AMP), and activities of H^+-ATPase, Ca^{2+}-ATPase and Mg^{2+}-ATPase were investigated in this work.

2. Materials and methods

2.1. Plant materials and treatments

Mature 'Fuyan' longan fruits were harvested from Fujian province, China. The tested fruits were treated as described in our previous study (Lin et al., 2014).

2.2. Determination of ATP, ADP and AMP contents

Contents of ATP, ADP and AMP were determined by applying the methods of Chen et al. (2014).

2.3. Determination of ATPase activity

ATPase were extracted from longan pericarp and determined following the modified methods of Lurie and Ben-Arie (1983), and Zhou et al. (2014). One gram pericarp tissue from ten longan fruit was grinded with 10 mL extraction medium [containing 5 mmol L^{-1} ethylene diamine tetraacetic acid (EDTA), 5 mmol L^{-1} dithiothreitol (DTT), 80 mmol L^{-1} Tris, 5% glycerol, 1 mmol L^{-1} benzyl sulfonyl chloride, 10 mmol L^{-1} vitamin C and 250 mmol L^{-1} sucrose, pH 8.9], then centrifuged under the condition of 1 2000*g* and 4 °C for 15 min. 0.2 mL supernatant was added to 0.5 mL reactant solution according to the types of ATPase and 0.2 mL 5 mmol/L ATP. After incubation at 36 °C for 10 min, the reaction was terminated by 0.2 mL of 20% (w/v) trichloroacetic acid and centrifuged under the condition of 6 000*g* and 4 °C for 10 min. Subsequently, 0.5 mL supernatant was added to 2.5 mL distilled water and ferrous sulfate-ammonium molybdate reagent. The absorbance value was measured at 660 nm after one minute.

The reactant solution H^+-ATPase contains 50 mmol L^{-1} Tris-HCl, 0.5 mmol L^{-1} KCl and 20 mmol L^{-1} $MgSO_4$. The reactant solution of Ca^{2+}-ATPase contains 50 mmol L^{-1} pH 7.5 Tris-HCl (pH 7.5), 50 mmol L^{-1}NaCl, 5 mmol L^{-1} DTT, 2 mmol L^{-1} $CaCl_2$ and 2 mmol L^{-1} EDTA. The reactant solution of Mg^{2+}-ATPase contains 0.05 mol L^{-1} Tris-HCl (pH 7.5), 50 mmol L^{-1} NaCl, 5 mmol L^{-1} $MgCl_2$, 2 mmol L^{-1} EDTA and 5 mmol L^{-1} DTT. ATPase which was sensitive to Na_3VO_4, KNO_3, and NaN_3 was plasma membrane ATPase, vacuole membrane ATPase and mitochondrial membrane ATPase, respectively. The final concentration of Na_3VO_4, KNO_3,

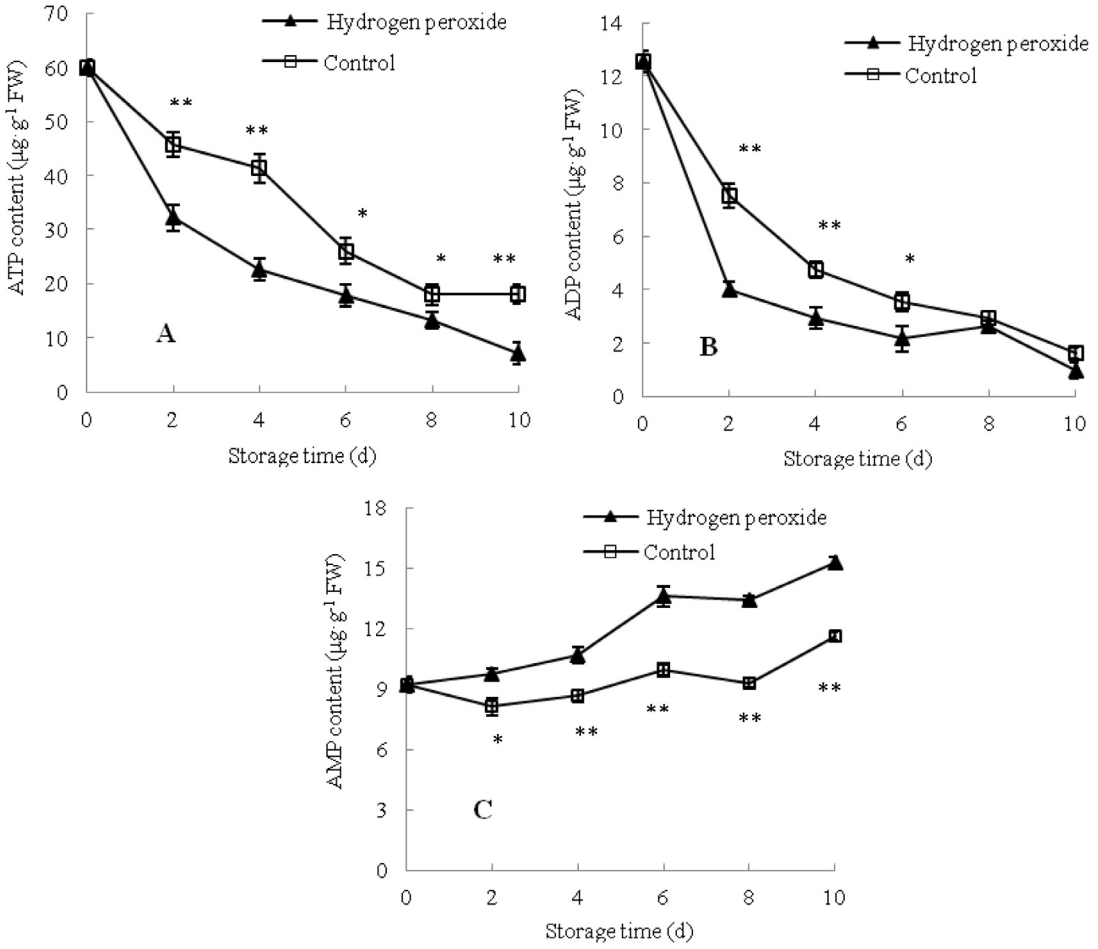

Fig. 1. Effects of hydrogen peroxide treatment on the contents of ATP (A), ADP (B) and AMP (C) in pericarp of harvested longan fruits. *Note:* The symbol (∗ and ∗∗) showed significantly difference according to the independent samples *t*-test ($P < 0.05$ and $P < 0.01$, respectively) for each time point. The same below.

and NaN_3 was 100 μmol L^{-1}, 50 μmol L^{-1} and 1 μmol L^{-1}, respectively.

One unit of ATPase activity referred to 1 μmol phosphorus released per hour at 660 nm. The method of Bradford (1976) was used to determine protein content. The unit of U·mg $protein^{-1}$ was used to express ATPase activity.

2.4. Statistical analyses

All assays were repeated in triplicate. Each value in figures represents the mean ± standard error (n = 3). Analytic variance was tested by SPSS version 17.0.

3. Results and discussion

3.1. H_2O_2-induced changes in contents of ATP, ADP and AMP in pericarp of harvested longan fruit

Adenosine triphosphate (ATP), mainly distributed in mitochondria, chloroplasts and cytoplasmic matrix, is the main source of energy for metabolism regulation (Jin et al., 2014). To a certain extent, the physiological status of plants can be measured by the level of ATP. The studies in recent years found that the energy deficit caused by declined ATP synthesis is one of the main causes for membrane damage and browning of postharvest horticultural products (Chen et al., 2014, 2015; Liu et al., 2015). Saquet et al. (2003) found that the drop in ATP content was the main cause of core browning in pears. However, exogenous ATP or pure oxygen could delay pericarp browning of litchi and longan by increasing energy level (Chen et al., 2015; Yi et al., 2010). In addition, the high ATP level contained in hydrogen sulfide-treated banana (Li et al., 2016), oxalic acid-treated peach (Jin et al., 2014) and brassinolide-treated bamboo shoot (Liu et al., 2016) benefited the maintenance of membrane integrity and alleviated the occurrence of pitting and browning, the two important characteristics of chilling injury.

As illustrated in Fig. 1, at harvest, longan fruit contained high levels of ATP and ADP, but relatively low AMP content. With the extension of storage, ATP and ADP levels reduced, whereas AMP content elevated. Accordingly, the linearity regression analysis indicated that the increased pericarp browning index (BI) (data had been published in previous study, Lin et al., 2014) of harvested longans showed a significantly reversed relation ($r = -0.9466$, -0.900, $P < 0.05$, respectively) with the rapid decrease in the contents of ATP (Fig. 1A) and ADP (Fig. 1B) ($y_{BI} = -0.097x_{ATP} + 6.633$, $y_{BI} = -0.392x_{ADP} + 5.379$, respectively), but a positive correlation with increased AMP level (Fig. 1C) ($r = 0.7218$, $y_{BI} = 1.033x_{AMP} - 6.570$). Furthermore, the decrease in ATP level of longan pericarp also showed a reversed relation ($y_{BI} = -1.267x + 89.26$, $r = -0.9252$, $P < 0.05$) with the increased ion leak of cell membrane indicating structural integrity of cell membrane (data had been published in previous study, Lin, Lin, Lin et al., 2016). Results above demonstrated the aggravated incidence of browning in longans pericarp was associated with the declined level of ATP, which was not beneficial to membrane integrity. In addition, H_2O_2-

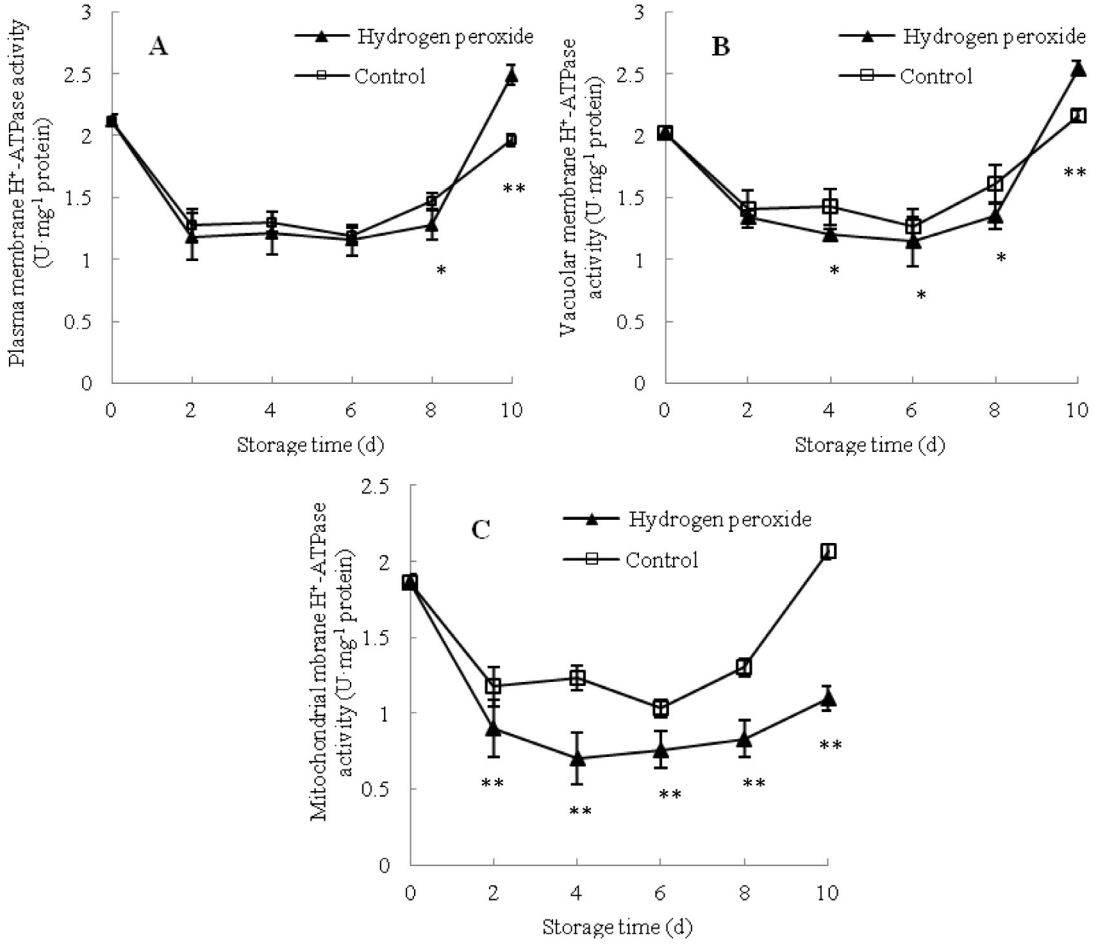

Fig. 2. Effects of hydrogen peroxide treatment on activities of H^+-ATPase in membranes of plasma, mitochondria and vacuole in the pericarp of harvested longan fruits.

treated longan fruit maintained lower contents of ATP (Fig. 1A) and ADP (Fig. 1B), but higher AMP content (Fig. 1C), pericarp browning index and ion leak rate (data had been published in previous study, Lin et al., 2014; Lin, Lin, Lin et al., 2016) compared with longans in control. These indicated that H_2O_2 accelerated the incidence of longan pericarp browning by enhancing the decrease in ATP, speeding up the process of membrane damage.

3.2. H_2O_2-induced changes in ATPase activity in pericarp of harvested longan fruit

Mitochondria are the main venue for oxidative phosphorylation and ATP production in cells (Jin et al., 2014; Morsomme & Boutry, 2000). Vacuole is responsible for the regulation of cell osmotic pressure and serves as the main pool of a variety of metabolites, such as phenolics, the substrate of enzymatic browning (Anil, Rajkumar, Kumar, & Mathew, 2008). H^+-ATPase, one kind of functional protein on cell membrane, can hydrolyze ATP to ADP and a free phosphate ion, with the release of energy as well as the establishment of the transmembrane electrochemical gradient and the transmembrane proton driving force. Meanwhile, ATP is synthesized under the catalytic of transmembrane proton electrochemical potential (Olsen et al., 2009). Magnesium (Mg) is a crucial cofactor of a variety of enzymes involved in respiration metabolism and energy metabolism (Nozadze et al., 2015). Furthermore, magnesium deficiency would induce over-saturation and oxidative stress (Tewari, Kumar, & Sharma, 2006). Calcium (Ca) can combine with pectic acid and phospholipid to maintain the structure and stabilization of cell wall and cell membrane (Yin et al., 2000). Ca^{2+}-ATPase and Mg^{2+}-ATPase are crucial for cellular homeostasis. They can utilize the energy from ATP hydrolysis to remove Ca^{2+} and Mg^{2+} from cytoplasm to extracellular environment or endomembrane organelles such as mitochondria and vacuole. The redundant accumulation of Ca^{2+} and Mg^{2+} in cytoplasm will break the environment balance and damage the structure of mitochondria, vacuole, and even the whole cell (Anil et al., 2008; Carafoli & Brini, 2000). Once their structures are damaged, their function will be in disorder and the synthesis of energy will be restrained. Thus, it will lead to energy deficiency and accelerate aging and death of plant (Jin et al., 2014; Morsomme & Boutry, 2000). Ghasemnezhad, Marsh, Shilton, Babalar, and Woolf (2008) reported that higher vacuolar H^+-ATPase and antioxidant enzymes levels were beneficial to protecting hot water-treated 'satsuma' mandarins against the development of dark colored irregular shaped pitting via the maintenance of energization and integrity of the vacuolar membrane. Pitting of blueberry fruit was suggested by Zhou et al. (2014) to be the result of decreased activities of mitochondrial H^+-ATPase and Ca^{2+}-ATPase, limited energy availability, and collapse of cytoplasm, plasma membranes and plastids. Moreover, applications of nitric oxide, oxalic acid and brassinolide alleviating chilling injury, featured by pitting and browning, of banana (Li et al., 2016), peach (Jin et al., 2014) and bamboo shoots (Liu et al., 2016) were due to the increased activity of mitochondrial H^+-ATPase and Ca^{2+}-ATPase, to maintain ATP content, energy charge and mitochondrial integrity. Therefore, it can be referred

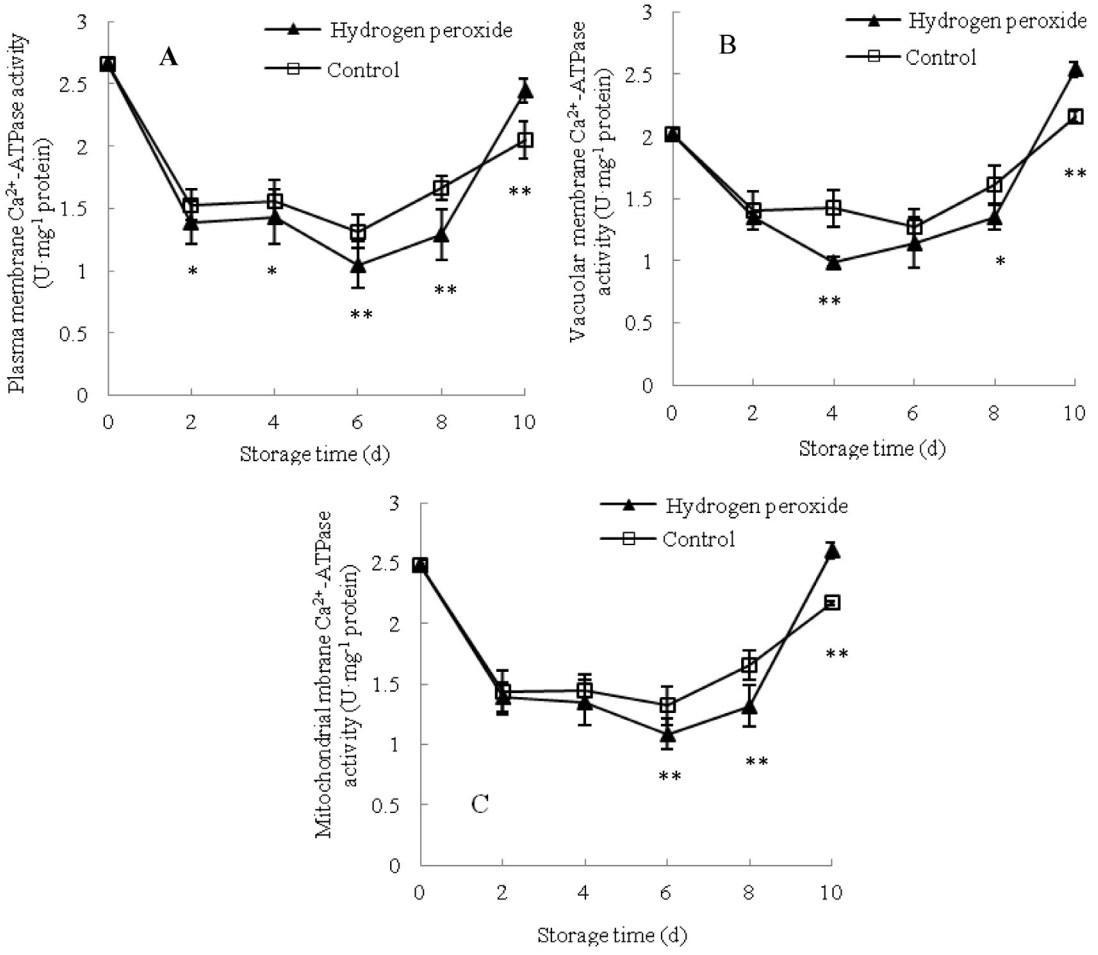

Fig. 3. Effects of hydrogen peroxide treatment on activities of Ca^{2+}-ATPase in membranes of plasma, mitochondria and vacuole in the pericarp of harvested longan fruits.

that ATPase activity in membranes of plasma, mitochondria and vacuole play an important part in browning of postharvest crops.

In this work, except for mitochondria membrane Mg^{2+}-ATPase, activities of H^+-ATPase (Fig. 2), Ca^{2+}-ATPase (Fig. 3) and Mg^{2+}-ATPase (Fig. 4) in membranes of plasma, vacuole and mitochondria in H_2O_2-treated longan were lower than those in control longan before the eighth day of storage. These data suggested H_2O_2-accelerated browning of longan pericarp could be attributed to the reduced H^+-ATPase activity, which might reduce the level of energy release and proton electrochemical gradient. Meanwhile conversely, the insufficient proton electrochemical gradient would reduce the synthesis of ATP, which was in agreement with reduced level of ATP content as shown in Fig. 1A. On the other hand, the reduced level of energy as well as the reduced activities of Ca^{2+}-ATPase (Fig. 3) and Mg^{2+}-ATPase (Fig. 4) would degrade the ability to squeeze out free Ca^{2+} and Mg^{2+} from cytoplasm or carry back to vacuole and mitochondria in H_2O_2-treated longan. The sustained increase of free $Ca^{2+}$and Mg^{2+} in cytoplasm might cause ionic imbalance and damage structure integrity of vacuole and mitochondria. The damaged mitochondria and vacuole would lead to the metabolic disorders of energy and respiration as well as the insufficient supply of energy, which would further damage the integrity of membrane in mitochondria, vacuole and the whole cell. Thus, this would induce the loss of cellular compartmentaliza-

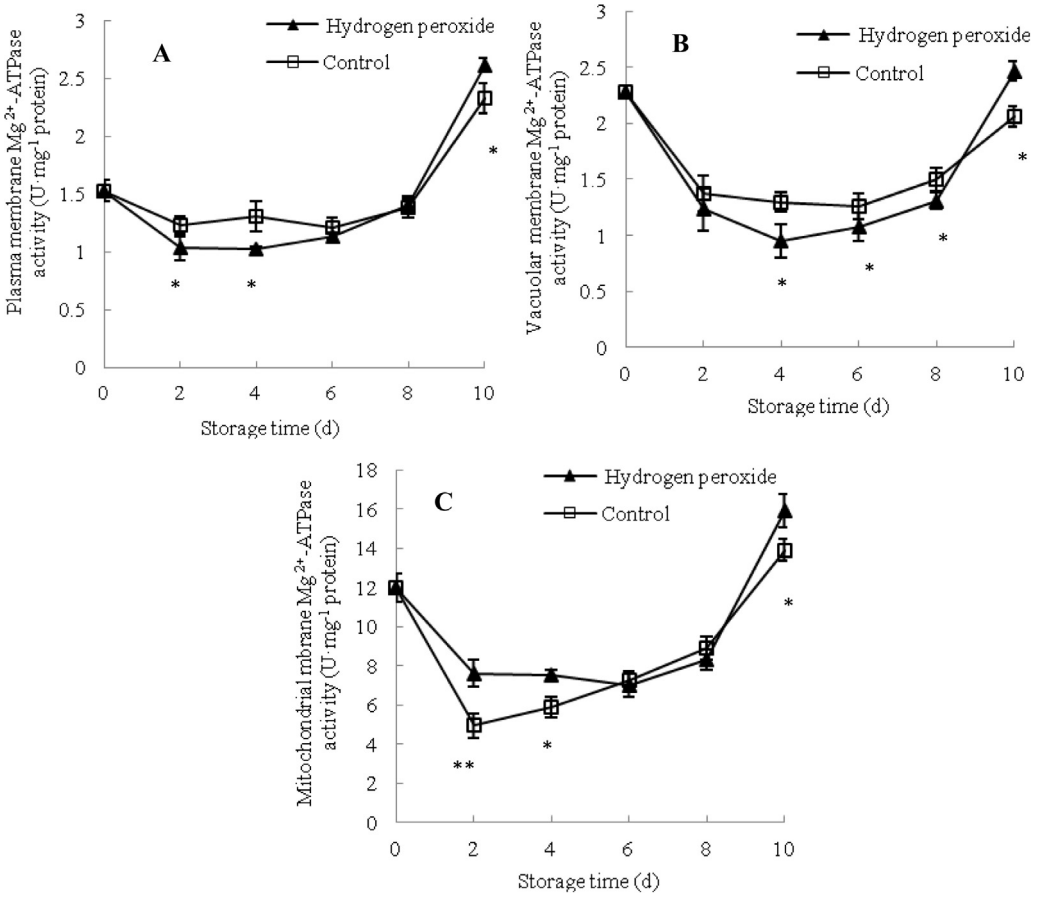

Fig. 4. Effects of hydrogen peroxide treatment on activities of Mg^{2+}-ATPase in membranes of plasma, mitochondria and vacuole in the pericarp of harvested longan fruits.

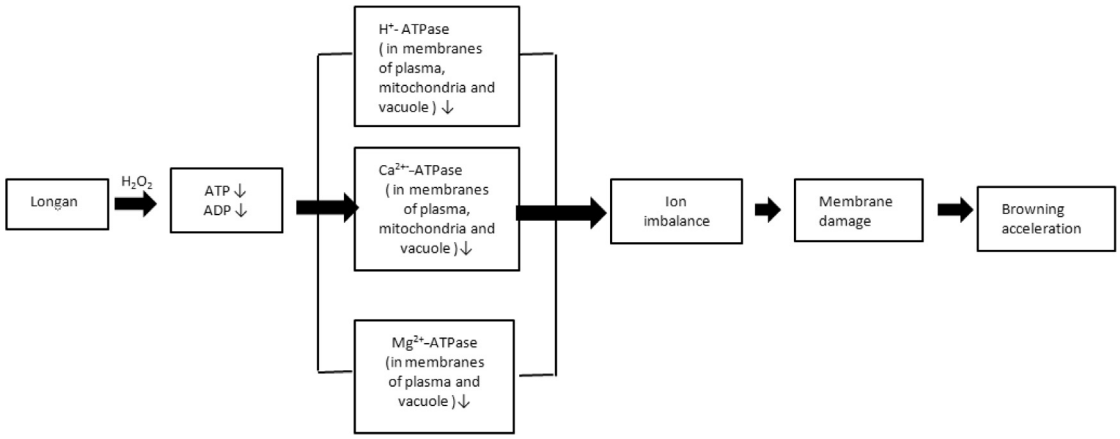

Fig. 5. The possible mechanism of hydrogen peroxide-induced pericarp browning of harvested longan fruit by acting on energy metabolism.

tion and the occurrence of browning of longan fruit during storage. This observation could be supported by our previous experiments, which showed that H_2O_2 could change respiratory metabolic pathways, reduce the energy charge and accelerate the degradation of fatty acids in cell membrane, resulting in limited energy availability and cellular de-compartmentalization (Lin, Lin, Lin et al., 2016; Lin, Lin, Chen et al., 2016). It was also found that, except for H^+-ATPase in mitochondrial membrane, the activities of H^+-ATPase (Fig. 2), Ca^{2+}-ATPase (Fig. 3) and Mg^{2+}-ATPase (Fig. 4) in membranes of plasma, vacuole and mitochondria in H_2O_2-treated longan were higher than the corresponding value in control fruit on day 10. This might be attributed to higher accumulation of intracellular protons, calcium and magnesium in H_2O_2-treated longan, which demanded for higher ATPase containing H^+-ATPase, Ca^{2+}-ATPase and Mg^{2+}-ATPase to remove protons, Ca^{2+} and Mg^{2+} from cytoplasm. Further comparison displayed that compared with Mg^{2+}-ATPase in membranes of plasma and valuoce (Fig. 4A, B), the activities of Mg^{2+}-ATPase in mitochondrial membrane (Fig. 4C) was highest, which demonstrated that mitochondrial membrane Mg^{2+}-ATPase took the first place to regulate intracellular and extracellular concentrations of Mg^{2+}. This was coincided with that mitochondria was the main organelle for respiration metabolism and energy metabolism, and Mg was essential for numerous enzymes related to these metabolisms.

4. Conclusion

In short, this study demonstrated that browning of harvested longans was closely associated with energy metabolism. The acceleration of pericarp browning caused by H_2O_2 might be due to H_2O_2 reducing levels of H^+-ATPase and Ca^{2+}-ATPase in membranes of plasma, mitochondria and vacuole, lowing activities of Mg^{2+}-ATPase in plasma membrane and vacuole membrane, and decreasing ATP level. These together may result in the imbalances of internal environment and the alterations of property and integrity in mitochondria, vacuole and the whole cell. These might directly or indirectly induce the disorders of metabolism, which, in turn, injuring to the cell membranes and organelles, and thus accelerating browning in pericarp of harvested longan fruit. However, the structure variation of mitochondria, vacuole and the whole cell after H_2O_2 treatment need further investigation. The possible mechanism of hydrogen peroxide-induced pericarp browning of harvested longan fruit by acting on energy metabolism was shown in Fig. 5.

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