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Phomopsis longanae Chi-induced pericarp browning and disease development of harvested longan fruit in association with energy status

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ABSTRACT

The effects of *Phomopsis longanae* Chi infection on browning development and disease incidence in relation to energy status in pericarp of harvested longan fruit were investigated. Longan fruit were inoculated for 5 min with *P. longanae* at 10^4 spores mL^{-1}, while fruit dipped in sterile deionized water were used as control. These fruits were stored at $(28 \pm 1)\,^{\circ}C$ and 90% relative humidity for up to five days. The results showed that the browning index, disease incidence, cellular membrane permeability and AMP content increased but the contents of ATP and ADP, and energy charge decreased in pericarp of longan fruit infected by *P. longanae*. It was suggested that *P. longanae* infection caused energy deficiency in longan fruit, possibly resulting in accelerated senescence and decreased resistance to pathogen, and thus promoted browning development and disease occurrence.

1. Introduction

Longan (*Dimocarpus longan* Lour.) is a non-climacteric tropical and subtropical fruit, which is grown commercially in many countries, especially in China, Thailand, Australia, Vietnam and some tropical and subtropical regions in the USA. China has the largest cultivation and production of longan fruit in the world, with 73.6% of the world's cultivated area and with 59.7% of the world's total output of longan (Jiang et al., 2002; Lin et al., 2013). Since longan fruit mature under high temperature and humidity, they deteriorate rapidly after harvest, due to pericarp browning and rot development caused by micro-organisms, which greatly restricts transportation, storage and market (Chen et al., 2011a,b; Duan et al., 2011).

Recent studies have shown that browning of harvested fruits and vegetables was characterized by energy deficiency due to decreased energy synthesis (Saquet et al., 2003; Veltman et al., 2003; Jiang et al., 2007; Shi et al., 2008; Yi et al., 2008a; Chen et al., 2009; Wang et al., 2013). Saquet et al. (2003) and Veltman et al. (2003) reported that energy status was a key factor in maintaining the integrity of cell membrane structure of 'Conference' pears, and that the declines in ATP content and energy charge were a possible reason accounting for brown heart in pears. Chen et al. (2009) found that 2,4-dinitrophenol (DNP), the uncouple agent for respiration, could block the formation of ATP. As storage time progressed, the ATP content in pericarp tissues of longan fruit after DNP treatment, decreased rapidly while the pericarp browning index rose sharply (Chen et al., 2009). Limited energy availability caused by DNP may lead to a reduced damage repair capacity of the cell membrane system, which may disrupt cell membrane structure, allowing phenolase (polyphenol oxidase, PPO) to react with phenolic substrates and then oxidize phenolics to form brown polymers (Duan et al., 2007; Chen et al., 2009). Application of exogenous ATP treatment could improve the energy status of litchi pericarp and help maintaining membrane integrity, which reduces decompartmented distribution of PPO and phenols resulting in pericarp browning (Song et al., 2006; Yi et al., 2008b). Moreover, disease development of harvested horticultural crops may be attributed to a limited supply of energy or low energy production (Saquet et al.,

Abbreviations: ATP, adenosine triphosphate; ADP, adenosine diphosphate; AMP, adenosine monophosphate; PPO, polyphenol oxidase; *P. longanae*, *Phomopsis longanae* Chi.

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2000; Qu et al., 2008; Yi et al., 2009). *Physalospora piricola* Nose as a major pathogen could account for fruit rot of 'Ya' pear, which mostly occurred under low energy status as the disease resistance of the fruit decreased, with a fastigium from 40 to 60 d after harvest, when ATP content in pulp of pears descended significantly (Wang et al., 2008). Cao et al. (2014) reported that depletion of ATP was associated with pathogen infection in the *Colletotrichum acutatum*-inoculated loquat fruit pathosystem. Treatment with methyl jasmonate (MeJA) maintained higher levels of ATP and energy charge in harvested loquat fruit during the storage time in association with inhibition of disease development on *C. acutatum*-inoculated fruit.

Our previous studies demonstrated that *Phomopsis longanae* Chi was the main pathogenic fungus inducing pericarp browning and fruit decay of harvested longan (Chen et al., 2011a,b). However, little information is available on pericarp browning and disease development induced by *P. longanae* infection regarding energy deficit. In this effort, *P. longanae* infection involved in contents of ATP, ADP and AMP, energy charge, and cell membrane permeability in pericarp of harvested longan fruit in relation to pericarp browning and fruit disease were investigated. The objective of the present study was to understand the role of energy status in browning and disease resistance loss in harvested longan fruit.

2. Materials and methods

2.1. Materials

P. longanae Chi was isolated, identified and preserved at the Institute of Postharvest Technology of Agricultural Products, Fujian Agriculture and Forestry University, Fuzhou, China. Fruit of longan (*D. longan* Lour.) cv. 'Fuyan' were harvested at mature stage from an orchard located in Nan'an city in Fujian province and transported to the Institute of Postharvest Technology of Agricultural Products on the harvest day. Healthy fruit selected for testing were uniform in size and color without mechanical injury, diseases, or insect pests.

Oat medium: the composition of the oat medium included 100 g oatmeal, 20 g powdered agar, and 1000 mL distilled water. This mixture was boiled for 30 min to dissolve the agar powder, and then sterilized under the pressure of 0.1 MP for 30 min after compensating for the water loss during boiling.

2.2. Treatments

The fruit were surface-sterilized with 70% alcohol for 5 s, then washed with sterile distilled water and finally divided into two groups randomly. The first group was immersed into sterile deionized water for 5 min and then used as control, whereas the second group was inoculated with *P. longanae* Chi for 5 min. *P. longanae* was isolated from infected longan fruit and then cultured on oat medium at 28 °C for 15 d. The spore suspension was diluted to a final concentration of 10^4 spores mL^{-1} by counting with a hemacytometer under a light microscope. All fruit were then air dried for about 60 min and packed separately in 20 plastic pallets (50 fruit per pallet), sealed with 0.015 mm thick polyethylene film bags, and then stored at (28 ± 1) °C and 90% relative humidity. Fruit sampling was conducted each day to evaluate pericarp browning and fruit disease, and determine physiological and biochemical indices during storage.

2.3. Evaluation of pericarp browning

The method of Lin et al. (2010) was employed to evaluate pericarp browning. Pericarp browning was assessed by measuring the extent of the total browned area of inner pericarp of 50 individual fruit using the following visual appearance scales: 1, no browning; 2, <1/4 browning; 3, 1/4–1/2 browning; 4, 1/2–3/4 browning; 5, >3/4 browning; and 6, complete browning. The browning index was calculated as Σ(browning scale × proportion of corresponding fruit within each class).

2.4. Evaluation of fruit disease

The method of Qu et al. (2006) was employed to evaluate fruit disease. Fruit disease was assessed by measuring the extent of the total lesion area of the fruit surface of 50 individual fruit according to the following visual appearance scale: 0, no lesion; 1, lesion area <1/4; 2, 1/4 ≤ lesion area <1/2; 3, 1/2 ≤ lesion area <3/4; and 4, lesion area ≥ 3/4. The disease index was calculated as Σ(disease scale/the highest scale × proportion of corresponding fruit within each class).

2.5. Determinations of contents of ATP, ADP and AMP and energy charge

Extractions and assays of ATP, ADP and AMP were conducted by applying the method of Ozogul et al. (2000) with a minor modification. Longan pericarp tissue (5 g from 10 fruit) was ground in liquid nitrogen to obtain a fine powder. The powder was then homogenized with 25 mL of 0.6 M perchloric acid. The homogenate was centrifuged at 16,000 × *g* for 10 min at 4 °C. The supernatant (10 mL) was quickly neutralized to pH 6.5–6.8 using 1 M KOH, and then diluted to 4 mL and passed through a 0.45 μm filter. Contents of ATP, ADP and AMP were measured by a Waters 2695 analytical high performance liquid chromatography with DAD detector (HPLC, Waters Corporation, USA) using a Megres™ C18 column (4.6 mm × 250 mm) and an ultraviolet detector at 254 nm. Mobile phase A consisted of 0.05 M dipotassium hydrogen phosphate and 0.05 M potassium dihydrogen phosphate dissolved in deionized water and then was adjusted to pH 7.0 with 0.1 M KOH. Mobile phase B was pure methanol. The elution was conducted by a linear gradient program with 85–100% A and 0–15% B for 35 min, with flow rate of 20 μL s^{-1}. Samples of 50 μL were injected into the HPLC. ATP, ADP and AMP contents were calculated according to the external standard program. Energy charge was calculated by [ATP + 1/2 ADP]/[ATP + ADP + AMP] (Su et al., 2005).

2.6. Measurement of membrane permeability

Membrane permeability was determined according to the method of Liu et al. (2007). Pericarp discs were removed with a cork borer (5 mm in diameter) from the equatorial region of 35 fruit. Fifty discs (about 2 g) were rinsed twice and then soaked in 25 mL of distilled water at 25 °C for 30 min. The electrolyte leakage (C_1) was determined with a conductivity meter (Model 3173, Shanghai Electronics Co., Ltd., China). Another batch of 50 discs was boiled for 15 min in 25 mL of distilled water and then cooled rapidly to 25 °C to assess total electrolytes (C_2). The relative leakage (%) was expressed as $(C_1/C_2) \times 100\%$.

2.7. Statistical analysis

The experiments were arranged in a completely randomized design, and each was comprised of three replicates. Data were tested by analysis of variance, using SPSS version 17.0. Least significant differences (LSD) were calculated to compare significant effects at the 5% or 1% level. Difference at $P < 0.05$ or $P < 0.01$ were considered significant or extremely significant, respectively.

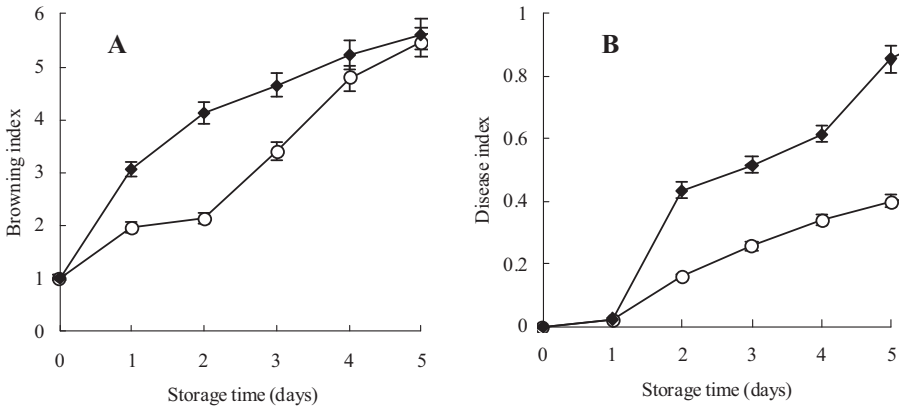

Fig. 1. Changes in browning index (A) and disease index (B) of longan fruit infected with *Phomopsis longanae* Chi. Vertical bars represent standard errors of means, $n = 3$. (○) control and (♦) inoculated.

3. Results

3.1. Effect of P. longanae Chi infection on browning development and disease incidence of harvested longan fruit

As shown in Fig. 1A, the browning index in pericarp of *P. longanae*-inoculated fruit increased rapidly in the first two days of storage, and then continuously rose slowly; while the index of control fruit increased slightly in the first two days and then rapidly. Statistical analysis indicated that the pericarp browning index of fruit infected by *P. longanae* was significantly higher ($P < 0.05$) than that of control from the first day to the fourth day of storage.

Fig. 1B shows that longan fruit were intact and basically non-susceptible within the first day of storage, but the disease index in *P. longanae*-inoculated fruit increased as storage time progressed. Lesions rapidly expanded and white mycelia grew on the epicarp. Five days from the inoculation treatment, the disease index was observed to be up to 0.85 and the whole pericarp was covered by lesions while the epicarp was overgrown by hypha; however, the disease index of control fruit increased only slightly and the disease index was 0.4. Statistical analysis indicated that the disease index of the fruit infected by *P. longanae* was extremely significantly higher ($P < 0.01$) than that of control fruit, which suggested that inoculation treatment could significantly increase pericarp browning and disease development in harvested longan fruit.

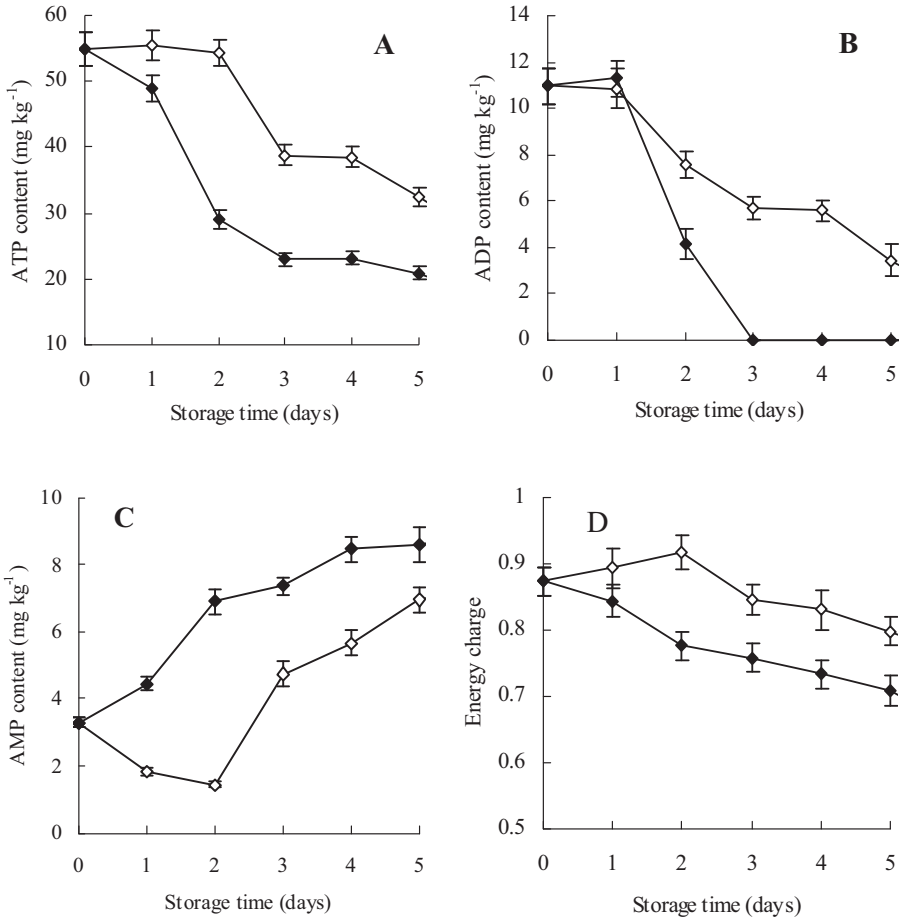

Fig. 2. Changes in ATP (A), ADP (B) and AMP (C) contents and energy charge (D) in pericarp of longan fruit infected with *Phomopsis longanae* Chi. Vertical bars represent standard errors of means, $n = 3$. (○) control and (♦) inoculated.

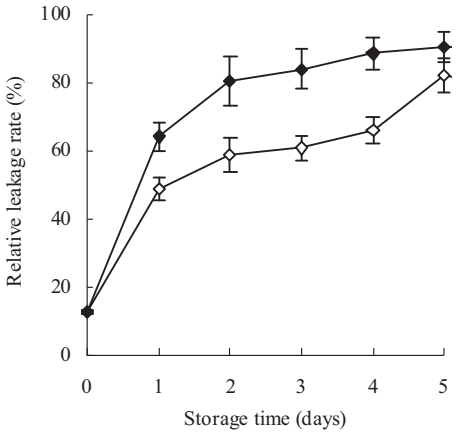

Fig. 3. Changes in relative leakage rate of pericarp of longan fruit infected with *Phomopsis longanae* Chi. Vertical bars represent standard errors of means, $n = 3$. (○) control and (♦) inoculated.

3.2. Effect of *P. longanae* Chi infection on contents of ATP, ADP and AMP and energy charge of harvested longan fruit

As shown in Fig. 2A, ATP content in *P. longanae*-inoculated fruit decreased rapidly within the first two days of storage and then declined slightly, but the control fruit did not show significant change in the ATP content over the first two days of storage, followed by a rapid decline on the third day and then gradual decrease. Statistical analysis indicated that ATP content of the fruit infected by *P. longanae* was extremely significantly lower ($P < 0.01$) than that of control fruit during storage.

The ADP content in pericarp of *P. longanae*-inoculated fruit declined sharply from the first day to the third day and was not detected on the third day. The ADP content of control fruit decreased rapidly from the first day to the third day and then declined gradually in the last two days of storage (Fig. 2B). Statistical analysis demonstrated that ADP content of the fruit infected by *P. longanae* exhibited an extremely significantly lower value ($P < 0.01$) than that of control fruit from the second day to the fifth day.

The longan fruit infected with *P. longanae* markedly increased AMP content over the first two days of storage and it stayed relatively high afterward. The AMP content in the control fruit declined during the first two days of storage and then rapidly increased (Fig. 2C). Significant differences in the AMP content existed between the *P. longanae*-inoculated fruit and control fruit during storage.

As shown in Fig. 2D, energy charge in the *P. longanae*-inoculated fruit declined as storage time progressed while it increased slightly in the first two days and then decreased rapidly in the control fruit. Moreover, the significant differences in the energy charge level between the *P. longanae*-inoculated and control fruit were observed.

3.3. Effect of *P. longanae* Chi infection on membrane permeability of harvested longan fruit

Cellular membrane permeability, expressed as relative leakage rate, can reflect the degree of plant cell senescence and damage (Lin et al., 2005). The relative leakage rate of cell membranes in longan pericarp tissues exhibited a tendency to rise with increasing storage time (Fig. 3). The relative leakage rate of the *P. longanae*-inoculated fruit increased rapidly in the first two days of storage and then went up slowly. The *P. longanae*-inoculated fruit exhibited a significant ($P < 0.05$) increase in the relative electrolyte leakage as compared to the control fruit. The results suggested that the infection with *P. longanae* accelerated the destruction of cell membrane structure in longan pericarp tissues.

4. Discussion

4.1. Pericarp browning induced by *P. longanae* infection related to energy deficit

Cell membrane damage during fruit browning might relate to the energy deficit (Jiang et al., 2007; Shi et al., 2008; Yi et al., 2008a). Previous studies showed that ATP played an important role in the biosynthesis of membrane lipids and cell membrane restoration. A direct relationship between energy metabolism and membrane integrity has been demonstrated in potato cells under anoxia by Rawyler et al. (1999) who found a threshold in ATP synthesis, below which potato cells became committed to hydrolysis of their membrane lipids, with increased production of hydrolysis product such as free fatty acid and N-acetyl phosphatidyl ethanolamine. As lipids are the essential components of cell membranes, the changes in membrane lipid constituents may lead to altered biophysical or biochemical membrane properties and result in loss of cellular compartmentalization as well as increases in ion leakage (Marangoni et al., 1996; Saquet et al., 2000). Su et al. (2005) reported that exposure to pure O_2 maintained membrane integrity of longan pericarp tissues, with high ATP content and high energy charge levels, and significantly prevented pericarp browning of longan fruit during storage. Moreover, an exogenous supply of ATP to litchi fruit can help maintain membrane integrity and reduce pericarp browning (Song et al., 2006; Yi et al., 2008b). Thus it can be inferred that ATP content and energy charge directly affect the integrity of cell membrane structure (Duan et al., 2004; Su et al., 2005; Liu et al., 2007; Yi et al., 2009), which could maintain cellular compartmentalisation, and thus, prevent polyphenol oxidase (PPO) coming into contact with phenolics resulting in enzymatic browning.

Under normal circumstances, tissues of fruit and vegetable can produce sufficient energy to support the regular physiological metabolism in cells. However, after suffering stress conditions including chilling injury (Yang et al., 2011) and pathogen infection (Yi et al., 2008b), ATP synthesis and energy status in plants cells is reduced, leading to the inability to meet energy needs for maintenance of proper physiological metabolism, which results in membrane degradation, cellular decompartmentation, and contact between PPO and phenolics to produce brown polymers (Jiang et al., 2004).

In the present work, high ATP and ADP contents and relatively low AMP content were observed in control longan fruit on harvest day (Fig. 2A–C). In the fruit inoculated with *P. longanae*, the contents of ATP and ADP and the energy charge decreased rapidly as storage time progressed (Fig. 2A, B and D) and the pericarp browning index and cell membrane permeability rose markedly (Figs. 1A and 3). Further comparison indicated that the ATP content and energy charge decreased within the first two days after *P. longanae* inoculation (Fig. 2A and D), but pericarp browning index and membrane permeability increased rapidly (Figs. 1A and 3). Correlation analysis showed that in the *P. longanae*-inoculated longan fruit held for five days of storage, there were significant negative correlations between browning index and ATP content ($r = -0.95$, $P < 0.01$), ADP content ($r = -0.905$, $P < 0.05$), and energy charge ($r = -0.967$, $P < 0.01$), but a significant positive correlation between browning index and AMP content ($r = 0.972$, $P < 0.01$). Thus, accelerated pericarp browning of longan fruit infected by *P. longanae* was closely related to the energy charge and contents of ATP, ADP and AMP in the adenylate pool. Furthermore, the energy deficit caused by low ATP level and energy charge of longan pericarp within the first two days after the infection was crucial for increased cell membrane permeability and accounted for pericarp browning of longan fruit during storage.

4.2. Postharvest disease of longan fruit related to energy deficit

The role of energy in the disease resistance loss of fruit and vegetable has drawn great attention. Recent studies have shown that disease development on harvested fruit and vegetable may be attributed to the short supply of energy or low energy production (Saquet et al., 2000; Yi et al., 2008a, 2009; Qu et al., 2008). For example, ATP level and energy charge in litchi pericarp decreased gradually with the fruit's senescence and disease progress (Duan et al., 2004; Yang et al., 2009; Liu et al., 2011; Wang et al., 2013). ATP content in pericarp of litchi fruit infected with *Peronophythora litchii* (a primary pathogen) increased as disease appeared, reaching its highest value at the initial disease stage, but then tended

to drop rapidly with the aggravating extent of disease (Yi et al., 2008b). Exogenous ATP treatment could contribute to energy status improvement and inhibition of browning in litchi pericarp during storage, as well as enhanced resistance against pathogen infection (Song et al., 2006; Yi et al., 2008b, 2009; Wang et al., 2013). Therefore, sufficient and effective energy may be a key factor in preventing harvested litchi pericarp browning, the loss of disease resistance and disease occurrence (Yi et al., 2010). Further study showed that the inhibitory effect of exogenous ATP supply on harvested litchi fruit infected with *P. litchii* may be due to the maintenance of high energy levels that inhibit the activity of membrane lipid degradation-related enzyme and reduce membrane lipid peroxidation of harvested litchi fruit during early storage (Yi et al., 2008a,b). In this effort, the study showed that higher ATP, ADP content, and energy charge were observed in longan fruit within the first day of storage and the energy charge and content of ATP and ADP in *P. longanae*-inoculated fruit decreased sharply with the aggravating extent of disease (Fig. 1B). Correlation analysis showed that in the *P. longanae*-inoculated longan fruit in the first five days of storage, there was significant negative correlation between disease index and ATP content ($r = -0.956$, $P < 0.01$), ADP content ($r = -0.932$, $P < 0.01$), and energy charge ($r = -0.977$, $P < 0.01$), but a significant positive correlation between disease index and AMP content ($r = 0.964$, $P < 0.01$). These results suggested that disease development or loss of disease resistance of longan fruit during storage could be accounted for by energy deficit.

In summary, infection with *P. longanae* decreased ATP synthesis and caused a low energy status in the pericarp of longan fruit, which may deteriorate cell membrane structure, damage decompartmentalization of PPO and phenolics, and cause enzymatic browning. Furthermore, limited availability of energy induced by *P. longanae* infection caused the loss of disease resistance and promoted disease occurrence of longan fruit.

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References

Cao, S.F., Cai, Y.T., Yang, Z.F., Joyce, D.C., Zheng, Y.H., 2014. Effect of MeJA treatment on polyamine, energy status and anthracnose rot of loquat fruit. Food Chem. 145, 86–89.

Chen, L., Chen, M.Y., Lin, H.T., Chen, Y.H., Lin, Y.F., Chen, S.J., 2009. Effects of uncouple agent DNP treatment on browning and active oxygen metabolism in pericarp of harvested longan fruit. Sci. Agric. Sin. 42, 4019–4026 (in Chinese with English abstract).

Chen, Y.H., Lin, H.T., Lin, Y.F., Zhang, J.N., Zhao, Y.F., 2011a. Effects of *Phomopsis longanae* Chi infection on browning and active oxygen metabolism in pericarp of harvested longan fruits. Sci. Agric. Sin. 44, 4858–4866 (in Chinese with English abstract).

Chen, Y.H., Lin, H.T., Lin, Y.F., Zhao, Y.F., Zhang, J.N., 2011b. Effects of *Phomopsis longanae* Chi infection on lipoxygenase activity and fatty acid constituents of membrane lipids in pericarp of harvested longan fruits. J. Trop. Subtrop. Bot. 19, 260–266 (in Chinese with English abstract).

Duan, X.W., Jiang, Y.M., Su, X.G., Liu, H., Li, Y.B., Zhang, Z.Q., Zheng, Y.H., Jiang, W.B., 2004. Role of pure oxygen treatment in browning of litchi fruit after harvest. Plant Sci. 167, 665–668.

Duan, X.W., Su, X.G., You, Y.L., Qu, H.X., Li, Y.B., Jiang, Y.M., 2007. Effect of nitric oxide on pericarp browning of harvested longan fruit in relation to phenolic metabolism. Food Chem. 104, 571–576.

Duan, X.W., Zhang, H.Y., Zhang, D.D., Sheng, J.F., Lin, H.T., Jiang, Y.M., 2011. Role of hydroxyl radical in modification of cell wall polysaccharides and aril breakdown during senescence of harvested longan fruit. Food Chem. 128, 203–207.

Jiang, Y.M., Duan, X.W., Joyce, D., Zhang, Z.Q., Li, J.R., 2004. Advances in understanding of enzymatic browning in harvested litchi fruit. Food Chem. 88, 443–446.

Jiang, Y.M., Jiang, Y.L., Qu, H.X., Duan, X.W., Luo, Y.B., Jiang, W.B., 2007. Energy aspects in ripening and senescence of harvested horticultural crops. Stewart Postharvest Rev. 3, 1–5.

Jiang, Y.M., Zhang, Z.Q., Joyce, D.C., Ketsa, S., 2002. Postharvest biology and handling of longan fruit (*Dimocarpus longan* Lour.). Postharvest Biol. Technol. 26, 241–252.

Lin, H.T., Xi, Y.F., Chen, S.J., 2005. The relationship between the desiccation-induced browning and the metabolism of active oxygen and phenolics in pericarp of postharvest longan fruit. J. Plant Physiol. Mol. Biol. 31, 287–297 (in Chinese with English abstract).

Lin, H.T., Chen, L., Lin, Y.F., Jiang, Y.M., 2010. Fruit weight loss and pericarp water loss of harvested longan fruit in relation to pericarp browning. Acta Hortic. 863, 587–592.

Lin, Y.F., Hu, Y.H., Lin, H.T., Liu, X., Chen, Y.H., Zhang, S., Chen, Q.X., 2013. Inhibitory effects of propyl gallate on tyrosinase and its application in controlling pericarp browning of harvested longan fruits. J. Agric. Food Chem. 61, 2889–2895.

Liu, H., Song, L.L., Jiang, Y.M., Joyce, D.C., Zhao, M.M., You, Y.L., Wang, Y., 2007. Short-term anoxia treatment maintains tissue energy levels and membrane integrity and inhibits browning of harvested litchi fruit. J. Sci. Food Agric. 87, 1767–1771.

Liu, H., Song, L.L., You, Y.L., Li, Y.B., Duan, X.W., Jiang, Y.M., Joyce, D.C., 2011. Cold storage duration affects litchi fruit quality, membrane permeability, enzyme activities and energy charge during shelf time at ambient temperature. Postharvest Biol. Technol. 60, 24–30.

Marangoni, A.G., Palma, T., Stanley, D.W., 1996. Membrane effects in postharvest physiology. Postharvest Biol. Technol. 7, 193–217.

Ozogul, F., Taylor, K.D.A., Qunantick, P.C., Ozogul, Y., 2000. A rapid HPLC determination of ATP-related compounds and its application to herring stored under modified atmosphere. Int. J. Food Sci. Technol. 35, 549–554.

Qu, H.X., Duan, X.W., Su, X.G., Liu, H., Jiang, Y.M., 2006. Effects of anti-ethylene treatments on browning and energy metabolism of harvested litchi fruit. Aust. J. Exp. Agric. 46, 1085–1090.

Qu, H.X., Yi, C., Jiang, Y.M., 2008. Loss of pathogen resistance by harvested horticultural crops. Stewart Postharvest Rev. 4, 1–4.

Rawyler, A., Pavelic, D., Gianinazzi, C., Oberson, J., Braendle, R., 1999. Membrane lipid integrity relies on a threshold of ATP production rate in potato cell cultures submitted to anoxia. Plant Physiol. 120, 293–300.

Saquet, A.A., Streif, J., Banerth, F., 2003. Energy metabolism and membrane lipid alterations in relation to brown heart development in 'Conference' pears during delayed controlled atmosphere storage. Postharvest Biol. Technol. 30, 123–132.

Saquet, A.A., Streif, J., Bangerth, F., 2000. Changes in ATP, ADP and pyridine nucleotide levels related to the incidence of physiological disorders in 'Conference' pears and 'Jonagold' apples during controlled atmosphere storage. J. Hortic. Sci. Biotechnol. 75, 243–249.

Shi, J.Y., Su, X.G., Li, Y.B., Qu, H.X., Jiang, Y.M., Duan, X.W., 2008. Inhibition of pure oxygen on pericarp browning of harvested litchi fruit in association with energy metabolism. Acta Hortic. 804, 339–346.

Song, L.L., Jiang, Y.M., Gao, H.Y., Li, C.T., Liu, H., You, Y.L., Sun, J., 2006. Effects of adenosine triphosphate on browning and quality of harvested litchi fruit. Am. J. Food Technol. 1, 173–178.

Su, X.G., Jiang, Y.M., Duan, X.W., Liu, H., Yi, Y.B., Lin, W.B., Zheng, Y.H., 2005. Effects of pure oxygen on the rate of skin browning and energy status in longan fruit. Food Technol. Biotechnol. 43, 359–365.

Veltman, R.H., Lentheric, I., Van der Plas, L.H.W., Peppelenbos, H.W., 2003. Internal browning in pear fruit (*Pyrus communis* L. cv Conference) may be a result of a limited availability of energy and antioxidants. Postharvest Biol. Technol. 28, 295–302.

Wang, H., Qian, Z.J., Ma, S.M., Zhou, Y.C., Patrick, J.W., Duan, X.W., Jiang, Y.M., Qu, H.X., 2013. Energy status of ripening and postharvest senescent fruit of litchi (*Litchi chinensis* Sonn.). BMC Plant Biol. 13, 1–16.

Wang, Y.N., Wang, G.X., Liang, L.S., Zhao, X.F., 2008. Effect of low temperature and pathogen stress during storage periods on pear fruit pulp ATP contents, H^+-ATPase and Ca^{2+}-ATPase activity. Sci. Silvae Sin. 44, 72–76 (in Chinese with English abstract).

Yang, A.P., Cao, S.F., Yang, Z.F., Cai, Y.T., Zheng, Y.H., 2011. γ-Aminobutyric acid treatment reduces chilling injury and activates the defence response of peach fruit. Food Chem. 129, 1619–1622.

Yang, E., Lu, W.J., Qu, H.X., Lin, H.T., Wu, F.W., Yang, S.Y., Chen, Y.L., Jiang, Y.M., 2009. Altered energy status in pericarp browning of litchi fruit during storage. Pak. J. Bot. 41, 2271–2279.

Yi, C., Jiang, Y.M., Shi, J., Qu, H.X., Duan, X.W., Yang, B., Prasad, N.K., Liu, T., 2009. Effect of adenosine triphosphate on changes of fatty acids in harvested litchi fruit infected by *Peronophythora litchii*. Postharvest Biol. Technol. 54, 159–164.

Yi, C., Jiang, Y.M., Shi, J., Qu, H.X., Xue, S., Duan, X.W., Shi, J.Y., Prasad, N.K., 2010. ATP-regulation of antioxidant properties and phenolics in litchi fruit during browning and pathogen infection process. Food Chem. 118, 42–47.

Yi, C., Qu, H.X., Jiang, Y.M., Duan, X.W., Cheng, G.P., Ruenroengklin, N., Yang, E., 2008a. Roles of energy in senescence and disease development of harvested litchi fruit. Acta Hortic. 804, 347–353.

Yi, C., Qu, H.X., Jiang, Y.M., Shi, J., Duan, X.W., Joyce, D.C., Li, Y.B., 2008b. ATP-induced changes in energy status and membrane integrity of harvested litchi fruit and its relation to pathogen resistance. Phytopathology 156, 365–371.