Received: 17 November 2023 | Accepted: 3 May 2024 | Published online: 9 June 2024

DOI: 10.1002/csc2.21274

Crop Science

HORTICULTURAL REVIEW

Litchi postharvest physiology and handling

Chao Chia Huang[1] | **Robert E. Paull**[2] | **Tsu-Tsuen Wang**[3]

[1]Crop Science Division, Taiwan Agricultural Research Institute, Wufeng, Taiwan

[2]Department of Tropical Plant & Soil Sciences, University of Hawaii at Manoa, Honolulu, Hawaii, USA

[3]Department of Horticulture and Landscape Architecture, National Taiwan University, Taipei, Taiwan

Correspondence
Robert E. Paull, Department of Tropical Plant & Soil Sciences, University of Hawaii at Manoa, Honolulu, HI, USA. Email: paull@hawaii.edu

Assigned to Associate Editor Irwin L. Goldman.

Funding information
National Institute of Food and Agriculture, Grant/Award Number: 58-2040-5-010

Abstract

Litchi (*Litchi chinensis* Sonn.) fruit, with its bright red color and sweet and juicy aril, is an important fruit crop in Asia, Africa, Australia, and South America. A major cause of the postharvest loss of litchi fruit is browning and decay. Chlorophyll breakdown and flavonoid synthesis occur simultaneously during the maturation of this nonclimacteric fruit. However, once litchi fruit is harvested, pericarp desiccation and membrane breakdown occur, which leads to browning with the rate of browning and later microcracking paralleling water loss rate. In addition, chilling injury can contribute to and increase pericarp browning and membrane leakage. Polyphenol oxidase and peroxidase are possibly key enzymes in the early stages of browning. An increase in the leakage of the pericarp membrane also occurs that correlates with browning. Many chemical treatments have been evaluated to retard pericarp browning, such as melatonin, hot water, acidified calcium sulfate (ACS), adenosine triphosphate, and tea seed oil. During long distance transportation, chemical treatments that involve sulfur are used, including SO_2 fumigation, acid dip after SO_2 fumigation, SO_2 fumigation and sulfur sheet package, or SO_2 fumigation followed by controlled atmosphere (CA), if approved by the importing country. Other treatments that avoid the use of SO_2 include melatonin, ACS, and hot water brushing combined with an acid dip, CA, and modified atmosphere packaging. Anthracnose is a common disease that accelerates browning and decay. *Penicillium* species as a saprophyte is also common with fruit infection occurring in the field, during harvest, in the packhouse, cold

Abbreviations: 1-MCP, 1-methylcyclopropene; AA, acetaldehyde; ABA, abscisic acid; ACC, 1-aminocyclopropane-carboxylic acid; ACO, 1-aminocyclopropane-carboxylic acid oxidase; ACS, acidified calcium sulfate; ADE, anthocyanin degradation enzyme; AEC, adenylate energy charge; AI, acid invertase; ALA, 5-aminolevulinic acid; AMP, adenosine monophosphate; ANT, anthocyanase; APX, ascorbate peroxidase; AsA, ascorbic acid; ATP, adenosine triphosphate; BAP, 6-benzylaminopurine; bHLH, basic helix-loop-helix protein; BOPP, bioriented polypropylene; CA, controlled atmosphere; CAT, catalase; CCO, cytochrome C oxidase; CHI, chalcone isomerase; CK, cytokinin; CPPU, 1-(2-chloropyridin-4-yl)-3-phenylurea; DFR, dihydroflavonol 4-reductase; DHAR, dehydroascorbate reductase; DNP, dinitrophenol; DPPH, 1,1-diphenyl-2-picrylhydrazyl; FRAP, ferric reducing antioxidant power; GABA, γ-aminobutyric acid; GPX, glutathione peroxidase; GR, glutathione reductase; GSH, glutathione; GST, glutathione sulfotransferases; LAC, laccase; LDPE, low-density polyethylene; LOX, lipoxygenase; MAP, modified atmosphere package; MDA, malondialdehyde; MDHAR, monodehydroascorbate reductase; PAL, phenylalanine ammonia lyase; PLD, phospholipase D; POD, peroxidase; PP, polypropylene; PPO, polyphenol oxidase; ROS, reactive oxygen species; SDH, succinate dehydrogenase; SMS, sodium metabisulfite impregnated sheet; SOD, superoxide dismutase; SPS, sucrose phosphate synthase; SSC, soluble solid content; TA, titratable acidity; TEAC, trolox equivalent antioxidant capacity; TSS, total soluble solid; UFGT, UDP-glucose: flavonoid 3-O-glucosyltransferase; VOC, volatile organic compound.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Authors. *Crop Science* published by Wiley Periodicals LLC on behalf of *Crop Science* Society of America.

rooms, and shipping containers. Sulfur sheet or CA is used to reduce fruit rot after SO_2 fumigation and Sportak (prochloraz) for the control of penicillium. However, a replacement for postharvest SO_2 use is still urgently needed.

1 | INTRODUCTION

Litchi fruit, with its bright red color and sweet and juicy aril, is an important fruit crop in Asia, Australia, Israel, Africa, and Central and South America (Menzel & Waite, 2005; Paull et al., 2014). Litchis are mainly produced in subtropics and the cooler tropics with adequate rainfall or irrigation. The variability of fruit supply from season to season and region to region leads to wide swings in available fruit supply and market price. These fluctuations in supply are due to the restrictive flowering and fruiting requirements of litchi and often alternate bearings that depend on cultivar, water availability, temperature, and a tree's vegetative status, coupled with the fruit's limited storage life of the fruit, and high consumer demand creates imbalances in the supply year to year.

Important litchi consumption areas are in temperate regions that have major population centers: Europe, North America, China, and Japan. Export is crucial to the development of the industry in many countries that are funneled through numerous export channels, such as litchis produced in China and Taiwan that are exported to the United States, Canada, Japan, and Singapore. Litchis produced in South Africa, Madagascar, Australia, and India can be exported to European markets such as France, Germany, and the United Kingdom (Mitra, 2002). Litchis from Thailand are exported to Hong Kong, Indonesia, Malaysia, Singapore, and Europe (Tongdee, 1998). Many of these export channels may involve 20–30 days or more for long distance sea transport and handling, or 7–12 days by air or for short distance sea transportation, such as Taiwan to Japan and Singapore. In addition, many countries have quarantine requirements mainly due to fruit flies that require an insect disinfestation treatment before entry. Current disinfestation treatments include application of a heat or cold treatment, or irradiation, that can lead to loss in fruit quality, especially pericarp browning. Pericarp browning and decay are major causes of postharvest quality loss in litchi fruit, irrespective of whether an insect disinfestation treatment is required (Akamine, 1960; Holcroft & Mitcham, 1996), and this browning has been the focus of much research.

Controlling litchi browning and decay has led to the commercial use of SO_2 fumigation (Swarts, 1983, 1985) and acid dip after SO_2 fumigation (Underhill, 1994; Zauberman et al., 1990, 1991). SO_2 treatment has human health concerns due to being an allergen for individuals suffering from asthma. In the United States, SO_2 is banned for cosmetic use (browning control), though approved as a fungicide. The replacement of SO_2 as a postharvest treatment has been continuously studied since the treatment was developed in the 1980s (Sivakumar et al., 2010). Research has ranged from searching for alternatives to the physiology, biochemistry, and molecular biology of this disorder. Enzymes such as polyphenol oxidase (PPO), peroxidase (POD), and anthocyanase (ANT) (Z. F. Lin, Li, Lin, et al., 1988; Z. F. Lin, Li, Zhang, et al., 1988; Underhill, 1992; Z. Zhang et al., 2001) and membrane factors including the oxidation and energy status (Duan et al., 2011; Y. Jiang, Duan, et al., 2004; Shi et al., 2008). More recently, molecular and biotechnology approaches have given us a greater understanding of these physiological and biochemical responses.

In this review, we will summarize the current status of this research as it relates to the nature of this nonclimacteric fruit where the edible flesh is an aril that grows from the funiculus, the surrounding pericarp sheet, postharvest changes, and current handling practices that impact fruit quality and postharvest storage life. We apologize to authors whose research is not cited due to manuscript length restrictions; these can be found as cited literature in the papers we have referenced.

2 | LITCHI CHEMICAL COMPOSITION AND NUTRITION VALUE

In the approximate analysis, moisture content, protein, lipids, carbohydrates (calculated by difference), and ash are determined. Four of the five are determined via chemical analysis, with carbohydrates being determined based on the other four. Carbohydrates would include at least dietary fiber and sugars. Analysis has evolved from the 1860s when it was developed in Germany to give a broad classification of food components. Nutritional analysis is much more detailed, and older methodologies are being replaced to meet national standards. Fruits, in general, are a good source of potassium, phosphorus, and vitamin C. Litchi has moderate amounts of calcium, magnesium, manganese, and copper.

2.1 | Moisture content

Litchi edible aril has a high moisture content that varies from 77% to 85% (Table 1) that varies by cultivar and production

year (Farina et al., 2017). The seed moisture content is about 54%, and the skin is 34% in ripe fruit.

2.2 | Sugars

Total soluble solids content (TSS), also called ˚Brix (%), is most commonly measured by differences in the refractive index, with distilled water used for calibration. The ˚Brix units honours Adolf Brix who developed hydrometers to measure sugar content in grams per 100 g solution (specific gravity) in wine, candy, and carbonated beverages. The degree ˚Brix is more appropriate for sugar solutions and less appropriate for the sugar content in fruits and fruit juices. Other soluble compounds including organic and amino acids, soluble pectins, and salts contribute to the refractive index (Crowther et al., 2005), and the extraction protocol can alter sugar composition (Cools & Terry, 2012), giving higher refractive index readings. The refractive index gives a useful approximation of sugar content expressed as % TSS. The in litchi of soluble solids content varies from about 14% to 21% mainly as sucrose, fructose, and glucose, with the ratio of sugars often dependent upon cultivar, the extraction protocol, and care to avoid invertase activity (Chan et al., 1975; Farina et al., 2017; Y. M. Jiang et al., 2006; Magwaza & Opara, 2015; Paull et al., 1984; Wall, 2006; H. C. Wang et al., 2006; Z. Yang et al., 2013).

The sugar content (sucrose, glucose, and fructose) varies widely between cultivars. Among 42 cultivars studied by Z. Yang et al. (2013), Shuangjianyuhebao, Jinzhong, and Wuyejiu had significantly less total sugars (<100 mg g^{-1} FW) than Zhuangyuanhong, Qingpi, Nuomici' Jidi, Feizixiao, and Wanpu (>150 mg g^{-1} fresh weight [FW]). Cultivars also varied in their hexoses/sucrose ratio from less than one to more than four with the difference being highly correlated with cell wall acid invertase, soluble acid invertase, and sucrose synthase. Earlier, H. C. Wang et al. (2006) classified the aril sugar composition of different cultivars into monosaccharide, disaccharide prevalent types, and intermediate types. Cultivars with low invertase activity and elevated activities of SS and sucrose phosphate synthase (SPS) accumulated sucrose as in Nuomici, while high invertase activity and lower activities of SS and SPS accumulate more reducing sugars Feizixiao (H. Wang et al., 2003).

Different amounts of mono and disaccharides and dietary fiber in fruits affect the glycemia index (GI) (Brand-Miller et al., 2009). GI is a measure of how rapidly carbohydrates in a food are digested and increase blood sugar levels, and this is a medical issue for an individual with type II diabetes. Values of GI between 0 and 55 are regarded as low, 56 and 69 moderate, and 70 and 100 high. Y. Y. Chen et al. (2011) showed that litchi had a moderate GI of 60 for people with type II diabetes and low (48) for healthy individuals; however, this difference was not found to be significant. In contrast, bananas have a GI of ~45, and mangos have a GI of 51. The other measure is the glycemic load (GL), which ranks food according to the amount of carbohydrates in a food that is eaten. Litchi is regarded to have a low GL being less than 10, with the understanding that less than 100 g of litchi aril is eaten with a GI of 60 at one sitting.

Core Ideas

- Litchi (*Litchi chinensis* Sonn.) in the Sapindaceae is a tropical fruit that is highly prized worldwide.
- The edible juicy aril is surrounded by a thin leathery pericarp.
- Major causes of postharvest loss are pericarp browning and decay.
- The cause and control of pericarp browning is a major focus of research.

2.3 | Acids

Taste is often expressed as a sugar-to-acid ratio. Acid increases sourness and decreases sweetness, while sugar increases sweetness and depresses sourness (Magwaza & Opara, 2015). The acid level in litchi increases during fruit development and then decreases during ripening (Joubert, 1986; Paull et al., 1984; H. C. Wang et al., 2006). The sugar-to-acid ratio ranges from 100 to 125 (Farina et al., 2017), which is indicative of the low acid content. The sugar/acid ratio therefore tends not to be as a useful quality indicator in this low acid fruit at full ripeness, when the sugar/acid ratio above 40, the fruit is regarded as having good eating quality (Underhill & Wong, 1990). As the fruit approaches full maturity and ripens, the sugar and particularly the acid content decrease as the aril undergoes its final growth, and this leads some cultivars to having a bland taste (H. B. Huang & Qiu, 1987).

The overall level of malic acid, the major acid (80%), Is low in ripe fruit (Chan & Kwok, 1974; H. C. Wang et al., 2006). This low acid level means that the TSS with the refractometer more accurately reflects the soluble sugars and sweetness of litchi. Smaller amounts of citric, tartaric, and oxalic acid are also found in litchi aril. Citric and oxalic acids are present during early fruit growth and are not detected in ripe fruit (H. C. Wang et al., 2006). Other reported acids include succinic, levulinic, glutaric, malonic, and lactic acids (Cavaletto, 1980; Paull et al., 1984) though not confirmed in more recent studies. Succinic acid is not the main organic acid present in litchi during fruit development (H. C. Wang et al., 2006), as previously reported (Paull et al., 1984).

TABLE 1 Proximate analysis of litchi aril flesh from the earliest recorded values (Higgins, 1917), recent published results, and the current values in USDA National Nutrition Database (2016) (Haytowitz et al., 2009).

Proximate	Higgins (1917)	Wenkam (1990) Guiwei	Wall (2006) (%) Kaimana (Heiye)	Cabral et al. (2014) Tailandes	Farina et al. (2017)—mean 4 cultivars	USDA (2016) per 100 g ± SE
Water	79.1	77.6	79.44	80.7	85	81.75 ± 1.01
Energy (kJ)		335		294		276
Protein (g 100 g^{-1} FW)	1.15	0.94		0.7	0.81	0.83 ± 0.04
Total lipids (g 100 g^{-1} FW)		0.29		0.8	0.81	0.44 ± 0.13
Ash (g 100 g^{-1} FW)	0.541	0.37		0.3	0.31	0.44 ± 0.05
Carbohydrates (g 100 g^{-1} FW)		20.77		15.3		16.53
Reducing sugars (g 100 g^{-1} FW)	12.5					
Sucrose (g 100 g^{-1} FW)	2.8					
Total sugars (g 100 g^{-1} FW)	15.3				11.8	15.23
Insoluble solids (g 100 g^{-1} FW)	1.79					
Fiber (g 100 g^{-1} FW)		1.6		2.2	1.17	1.3
Minerals (mg 100 g^{-1} FW)						
Calcium		4	3.1	1.8	8.5	5 ± 1
Iron		0.37	0.28	0.86	0.13	0.31 ± 0.06
Magnesium		16	13.7	12.9	11.9	10
Phosphorus		35	28.8	39.0	19.8	31 ± 3
Potassium		255	130.7	106.7	135	171 ± 23
Sodium		7	3.1	5.9	5.45	1
Zinc			0.24	0.22	0.76	0.07
Copper			0.20	0.12	0.5	0.15
Manganese			0.05	0.06	0.15	0.06
Selenium				0		0.6
Vitamins						
Vitamin C, total ascorbic acid (mg)		40.2	30.66	34.7	57.66	71.5 ± 10.2
Thiamine (mg)		0.035			0.027	0.011
Riboflavin (mg)		0.084			0.067	0.065 ± 0.009
Niacin (mg)		1.91			1.16	0.603 ± 0.147
Vitamin B6 (mg)						0.1
Folate total (μg)						14
Choline total (mg)						7.1
Vitamin E (alpha-tocopherol) (mg)				0.128		0.07
Vitamin K (phylloquinone) (μg)						0.4

Note: No vitamin B-12, vitamin A, retinol, carotene (beta), carotene (alpha), cryptoxanthin (beta), vitamin A, lycopene, and lutein + zeaxanthin recorded.
Abbreviation: FW, fresh weight.

2.4 | Ascorbic acid

Litchi is recommended as a good source of vitamin C (ascorbic acid). The vitamin C content ranges from 30 to 70 mg 100 g^{-1} (Table 1). The early-maturing Hawaiian litchi cultivar Kaimana, a selection from Heiye, shows an average vitamin C content of 33 mg 100 g^{-1}, while the late-maturing Groff (Shui dong) and Bosworth-3 (Gui wei) had 21 and 23 mg 100 g^{-1}, respectively (Wall, 2006). Mauritius (Dazao) and Mc Lean's Red (possibly selection Indian cultivar of selection Purbi) have 27 and 21 mg 100 g^{-1}, respectively (Sivakumar, Naudé, et al., 2008). Vitamin C levels are very high early in fruit growth and decline as the fruit approaches maturity and ripens and remain constant in the last few weeks before the ripe stage (H. C. Wang et al., 2006). When cultivars were compared in the same study, considerable variation in Vitamin C content has been reported; for example, Feizixiao has 41 mg 100 g^{-1}, while Nuomici has 19 mg 100 g^{-1} (H. C. Wang et al., 2006).

2.5 | Minerals

The litchi fruit is a good source of potassium (K) and nitrogen (N) (Table 2). The content of N, P, K, Ca, Mg, Na, and Fe vary widely and may reflect different cultivars and preharvest growing conditions. The results of Wall (2006) and Farina et al. (2017) clearly indicate both cultivars, production season, and production area affect mineral content.

2.6 | Protein, lipids, and fiber

Litchi aril, like most fruit, is low in total protein and lipids (Cavaletto, 1980; Farina et al., 2017; Pareek, 2018) with only 0.7%–1.0% protein in aril on a fresh weight basis (Table 1) (Farina et al., 2017; Watt & Merril, 1963). Similarly, total lipids are also less than 0.1% on a fresh weight basis (Farina et al., 2017; Watt & Merril, 1975). Total dietary fiber ranges from 1.1% to 1.25% (Farina et al., 2017). Only small amounts of free amino acids are detected with γ-aminobutyric acid (GABA) (Z. C. Wu et al., 2016), with aspartic acid, glutamine, asparagine, serine, glutamine, arginine, alanine, tyrosine, valine, and methionine being found in much lower concentrations.

Considerable variation is seen in the aril content of these constituents (proteins, lipids, and fiber) (Table 1). The difference may be due to cultivar (Farina et al., 2017; A. Singh et al., 1987), year, and location of production (Farina et al., 2017; A. Singh et al., 1987; Tripathi et al., 1987).

2.7 | Active substances

Litchi contain several nutritional and functional components in addition to vitamins and phenolic compounds (Table 1) (D. Su et al., 2014; Z. C. Wu et al., 2016). Antioxidants scavenge free radicals and therefore are potentially involved in human health. Plant compounds thought to be responsible for these protective effects include carotenoids, antioxidant vitamins (ascorbic acid and tocopherols), phenolics, flavonoids, proanthocyanidins, and anthocyanins. Litchi exhibit higher antioxidant activity in ferric reducing antioxidant power (FRAP) than in the Trolox equivalent antioxidant capacity (TEAC) assay (Luximon-Ramma et al., 2003). Total phenolics are 288 μg g^{-1} FW as gallic acid equivalents, flavonoids 94 μg as quercetin equivalents g^{-1} FW, proanthocyanidins 100 μg cyanidin chloride g^{-1} FW, TEAC of 5 μmol Trolox g^{-1} FW, and FRAP of 3 μmol Fe(II) g^{-1} FW. The ascorbate content and antioxidant capacity (TEAC and FRAP) are poorly correlated. The largest proportion of the antioxidant in litchi aril is associated with total phenolics through FRAP and 2,2-diphenyl-1-picrylhydrazyl (DPPH) assays (Saxena et al., 2011; Septembre-Malaterre et al., 2016). The three phenolic compounds that are the major contributors to antioxidant activity in litchi aril are quercetin 3-O-rutinoside-7-O-a-l-rhamnosidase, quercetin 3-O-rutinoside (rutin), and (-)-epicatechin at 70.35%, 14.60%, and 9.42%, respectively (D. Su et al., 2014). Also detected are gallic acid, chlorogenic acid, (+)-catechin, and caffeic acid at less than 500 μg/100 g of FW (D. Su et al., 2014; R. Zhang et al., 2013). Significant differences in antioxidant activity are observed between cultivars using FRAP and DPPH scavenging capacity methods (Saxena et al., 2011; R. Zhang et al., 2013).

In addition to ascorbic acid and phenolics, litchi also contain myo-inositol (0.28–0.78 mg g^{-1} FW), GABA (1.7–3.5 mg g^{-1} FW), and L-quebrachitol (1.6–6.4 mg g^{-1} FW); these ranges are from analysis of 10 different cultivars (Z. C. Wu et al., 2016). Litchi is regarded to have a moderate amount of myo-inositol. Myo-inositol has been associated with several neurological conditions. Fresh vegetables and fruits contain more myo-inositol than other foods and are the main dietary source in our diet (Clements & Darnell, 1980). The GABA concentration in litchi aril is nearly 100 times greater than in other fruits and L-quebrachitol not being common in most fruits. GABA is a nonprotein amino acid with a role in mammalian central nervous system (Foster & Kemp, 2006). The content in litchi aril is about a hundred times higher than in other fruits and 25–55 times higher than the second most abundant amino acid (glutamic acid) in litchi.

Adverse food reactions have been reported to litchi consumption and have been explained as an allergic reaction (Fär et al., 1995; Hoppe, Neidhart, et al., 2006; Hoppe, Steinhart, et al., 2006; Raap et al., 2007; Saraswat & Kumar, 2005; Y. Wang et al., 2009; X. Wang et al., 2016). Symptoms after eating include itchy or sore throat, swelling of the lips and throat, labored breathing, or diarrhea. Profilin (Fär et al., 1995; Song et al., 2007) and a triose-phosphate isomerase (Hoppe et al., 2006b) have been implicated in this reaction. Cross reactivity to latex (Niggemann et al., 2002) and with other fruits (Saraswat & Kumar, 2005) has also been reported.

3 | LITCHI VOLATILES

Volatile organic compounds (VOCs) are metabolites released by plants into the air. The VOCs released by fruits are reported to be up to 20% of the total CO_2 fixed each day by plants (Baldwin, 2010). The volatiles are used to protect plants against abiotic and biotic stresses, plant-to-plant communication, and to provide information for pollination and seed dispersal. In the case of fleshy fruits, volatile release along with color changes are cues to fruit ripeness to attract seed dispensers such as frugivorous birds, bats, and other animals to move seed away from the parent plant (Bouwmeester et al., 2019; Rodríguez et al., 2013; Tiffney, 2004;

TABLE 2 Mineral composition of selected litchi cultivars (Mg 100 g^{-1} of FW).

Cultivar	Pinyin	Country	K	P	Ca	Mg	Na	Fe	Cu	Zn	Mn	B	Reference
Groff	Shuidong	Hawaii[a]	140	22	3	19	ND	ND	ND	ND	ND	ND	Paull et al. (1984)
Bosworth	Guiwei	Hawaii	160–172	24–25	2–5	12–13	3-7	0.36– 0.43	0.17–0.20	0.16–0.26	0.05–0.07	0.09–0.11	Wall (2006)
Groff	Heiye?	Hawaii	140	28	5	16	8	0.41	0.23	0.28	0.11	0.12	Wall (2006)
Kaimana	Heiye selection	Hawaii	131–181	27–31	3–6	14–16	3–5	0.28–0.38	0.17–0.20	0.19–0.26	0.05–0.10	0.13–0.16	Wall (2006)
Mauritius	Dazao	South Africa	178	35	4.9	13.2	4.1	0.4	0.17	0.23	0.12	0.09–0.11	Sivakumar, Naudé, et al. (2008)
McLean's Red	?	South Africa	182	31	3.8	10.3	3.2	0.21	0.18	0.18	0.33	0.09–0.11	Sivakumar, Naudé, et al. (2008)
Brewster	Chenzi?	Sicily[b]	136	17.9	8.2	9.4	5.2	0.09	0.38	0.45	0.12	ND	Farina et al. (2017)
Kwai Mai	Guiwei	Sicily[b]	164	16.8	7.9	16.9	5.1	0.12	0.54	0.92	0.13	ND	Farina et al. (2017)
Tai So	Dazao	Sicily[b]	241	27.8	9.8	11.2	6.3	0.18	0.53	1.15	0.22	ND	Farina et al. (2017)
Wai Chee	Huaizhi	Sicily[b]	135	16.7	8.1	10.3	5.2	0.11	0.55	0.55	0.12	ND	Farina et al. (2017)

Abbreviation: ND, not determined.

[a]Results originally presented on a dry weight basis, adjusted to 85% moisture content.

[b]Results originally presented on a dry weight basis, adjusted to 86.07% for Brewster, 84.83% for Kwai Mai, 83.87% for Tai So, and 85.89% for Wai Chee moisture content in year 1 (Farina et al., 2017).

Valenta et al., 2013). Plant volatiles are made up of a wide range of low-molecular weight secondary metabolites with appreciable vapor pressure under ambient conditions. The diversity can be seen from the four major biosynthesis pathways, all of which are involved in the generation of litchi volatiles: (i) the acetate pathway leading to C18 fatty acids and jasmonic acid and C6 alcohols and their esters; (ii) the melavalonic acid pathway leading to sesquiterpenoids; (iii) the methylerythritol pathway leading to mono-, di- and triterpenoids; and (iv) Shikimate pathway for benzenoids and phenolics (Bouwmeester et al., 2019). Comparison of volatiles is complicated because of the complexity of the blend of volatiles emitted and the fact that only a few of these volatiles may be major aroma key volatiles recognized by humans. These key impact volatiles may not be a major volatile component emitted. In litchi, the floral aroma is more pronounced than the fruity notes.

Litchi aroma is normally described as rose and fruity-floral, and one of the earliest studies found 42 volatiles (Johnston et al., 1980). The main constituents are β-phenethyl alcohol and its derivatives and terpenoids with certain terpenoids comprising the major portion of the volatiles. Subsequently, other workers identified additional volatiles that reported alcohols, carbonyl compounds, ethers, esters, ketones, and terpenes. The conclusion drawn is that the fruity flavor (citrus-like) is associated with methyl esters of various alcohols, and acetates of limonene, nonanal, decanal, citronellyl, and geranyl. Monoterpene (rose oxide) is responsible for rose fragrance (Chyau et al., 2003; Froehlich &, Schreier, 1986; Ong & Acree, 1998; Toulemonde & Beauverd, 1985).

Varietal differences in volatile profiles are found (Chyau et al., 2003; Sivakumar, Naudé, et al., 2008). For example, no esters are detected in McLean's red (Bengal) while present in Mauritius (Dazao) with zingiberene being the predominant sesquiterpene and terpinolene the most abundant monoterpene in Mauritius, with rose oxide, limonene, citronellol, and geraniol being at low levels (Sivakumar, Naudé, et al., 2008). Y. Wu et al. (2009) compared nine litchi cultivars from southern China, and 96 volatiles were detected, with mass spectroscopy identifying 43 with another 53 given tentative identification. Identified were 35 terpenoids, 27 alcohols, 10 aromatic compounds, nine aldehydes, eight esters, four ketones, two sulfur compounds, and one organic acid. Common volatiles found included linalool, cis-rose oxide, α-terpineol, β-citronellol, geraniol, ρ-cymene, ethanol, 3-methyl-3-buten-1-ol, 3-methyl-2-buten-1-ol, 1-hexanol, (E)-2-hexen-1-ol, 2-ethyl-1-hexanol, 1-octen-3-ol, 1-octanol, ethyl acetate, ρ, α-dimethylstyrene, and 3-tert-butyl-4-hydroxyanisole. The varieties "Guangxi Huaizhi" emitted the most diverse profile with 67 volatiles and Jizuili the least (36 volatiles). The highest odor components are commonly cis-rose oxide, trans-rose oxide, 1-octen-3-ol, and geraniol. The authors also showed that the variety "Huaizhi" from two production areas had similar volatile profiles. A more recent study using gas-chromatography mass spectroscopy coupled with olfactometry (Feng et al., 2018) found 31 active odor active components (key aroma components) that overlap with earlier results. In the Florida variety "Sweetheart," (Fezixiao), they found methional, geraniol, furaneol, nerol, dimethyl trisulfide, linalool, (E, Z)-2,6 non-adienal, and nerolidol. In addition, these researchers identified nerolidol and homofuraneol as odor-active components for the first time in litchi. These findings complement and extend the results of Y. Wu et al. (2009) as to the odor-active components in litchi.

4 | POSTHARVEST PHYSIOLOGY

4.1 | Fruit development and mature

4.1.1 | Fruit growth and composition

The growth curves of the pericarp, seed, and aril and the fruit as a whole were typically sigmoidal (H. B. Huang & Xu, 1983). The growth of fruit and arils shows a sigmoidal pattern, while the growth is slower and more linear (Figure 1a). Rapid growth is principally due to an increase in aril tissue (Paull et al., 1984). Fruit length increased up to the 17^{t}h week from anthesis, while width and weight increased continuously. The percentage of pericarp, as a portion of the fruit, decreased until the 17^{t}h week, while the percentage of aril increased until the 19^{t}h week (Rivera-López et al., 1999). The percentage of aril varies between varieties (H. C. Wang et al., 2017; Yen, 1983) in relation to seed development. Three types of fruit are seen: normal with a viable embryo, aborted, and seedless. Few varieties such as "Wuheli" are seedless (parthenocarpic). Fruit with aborted seeds (Figure 1b), often referred to as "chicken tongue" (stenospermocarpy) have small poorly developed embryos and shriveled seeds (Yen, 1983), and has been associated with seed cell wall invertase gene expression (Zhang, Wu, et al., 2018). The proportion of aborted seeds varies between individual trees in the same orchard, with variety the "Nuomici" having a high proportion of aborted seeds (H. C. Wang et al., 2017; Yen, 1983), year-to-year, unfavorable weather (R. A. Stern & Gazit, 1996), and self-pollination versus cross-pollination (R. A. Stern et al., 1993). Fruit with aborted seeds are prized by consumers because of their higher aril-to-seed ratio, though the amount of aril in each fruit is the same (Yen, 1984).

Pericarp chlorophyll began to decline logarithmically soon after the start of fruit growth increase, with anthocyanin production beginning about halfway through the growth period. Total sugars increase in aril from 3% to 16% during the rapid growth period. Aril acidity decreases over 2 weeks in the middle of fruit growth (Paull et al., 1984). Titratable acidity (TA) is mainly due to malic acid. As the fruit matures, the size

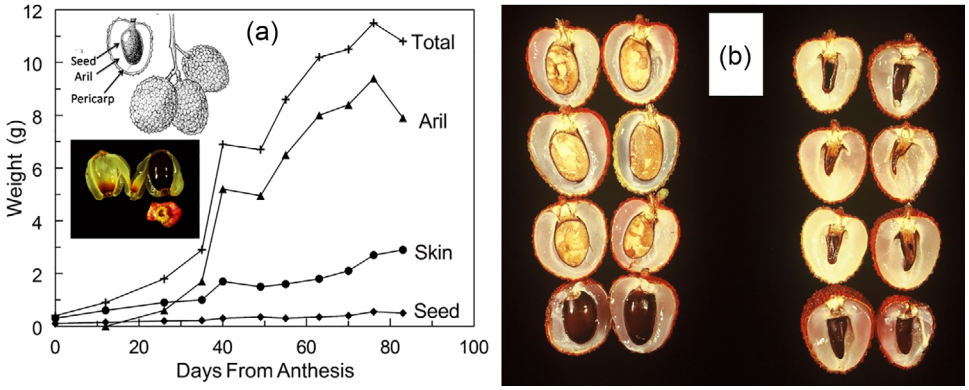


FIGURE 1 Litchi fruit development: (a) growth of fruit component parts from anthesis, and (b) difference in seed size due to arrested seed development with continued aril as an outgrowth from the funiculus. Arrested seed development leads to a significantly higher flesh to seed ratio and is highly desired. Fruit component growth redrawn from Paull et al. (1984).

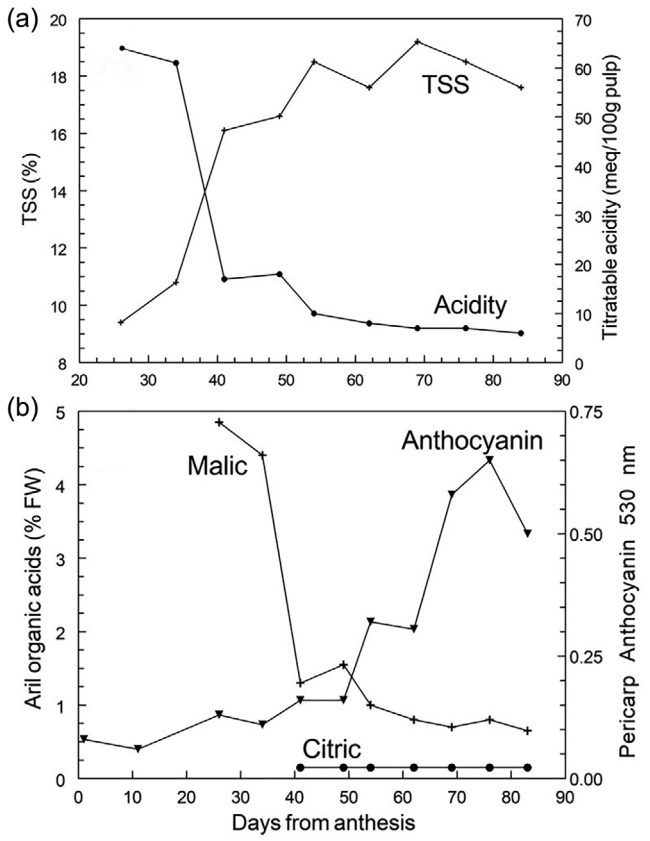


FIGURE 2 Changes during litchi fruit development: (a) changes in total soluble solids (TSS) (%) and titratable acidity and (b) changes in the component acids in the aril and changes in pericarp anthocyanins as absorbance at 530 nm. Redrawn from Paull et al. (1984).

of the fruit increased, TSS in pulp increases, TA decreases (Figure 2a), resulting in an increase in TSS/TA ratio, ethanol content increases, while the lightness (CIE $L*a$) and the firmness decrease (Reichel et al., 2010). The malic acid in aril shows a dramatic decline as the fruit ripens with an increase in pericarp anthocyanins (Figure 2b).

This nonclimacteric fruit does not continue to ripen after harvest and is harvested when fully ripe (Kader, 1998; Paull et al., 2014). Cultivar-specific fruit colour changes, fruit shape, pericarp texture, and flavour are the maturity indexes that are used the most. Objective aril TSS and TA readings are often determined, and their ratio is used as a more accurate maturity index by the South African Litchi Growers' Association. In Australia, the TSS/TA ratio of 30:1 to 40:1 is recommended (Underhill & Wong, 1990). In Israel, a lower minimum TSS/TA ratio of 20:1 is used at maturity, and more than 29:1 indicates fruit is overripe (Sivakumar et al., 2010). South Africa recommends the TSS/TA ratio to be 25:1, and the TSS/TA should be between 20:1 and 30:1 for HLH Mauritius and McLean's Red that are sulfur fumigated before export. The fruit has relatively few fungal infections during export simulations when the TSS/TA ratio was lower than 30:1. The incidence of infection increased dramatically when the TSS/TA ratio became higher than 30:1. Furthermore, the over-mature McLean's Red litchi also had significantly higher SO_2 residues in the aril of the fruit (Schoeman et al., 2004). Hong Huey harvested in pink to the red-shelled stage, and Chacapat at the pink-shelled stage provided optimum eating quality in long supply chains (Reichel et al., 2010).

Litchi harvested in the early morning (4 to 6 a.m.) when it is cool exhibited the least weight loss and browning index, and maximum anthocyanin content, as well as marketable fruit (74%). The fruit were stored at ambient temperatures for 5 days in 2-kg ventilated corrugated fiberboard boxes with a perforated polymer liner (Purbey et al., 2018). The fruit harvested later in the morning (9 to 12 a.m.) had only 62% marketable fruit with a lower thickness of the pericarp, moisture content, $a*$ value, and the highest respiration rate.

More mature fruit has greater pericarp membrane leakage than less mature and earlier harvested fruit (X. M. Huang et al., 2005). Cuticle thickness also decreased from 8.75 to 1.88 μm as the fruit matured (Underhill & Critchley, 1992), which might explain the increase in pericarp water loss and

browning. As maturity increases, the alcohol content in pulp increases and firmness declines (Reichel et al., 2010). Pesis et al. (2002) harvested fruit from early to late in the season and divided each batch into four maturity levels according to colour. The higher the maturity of the fruit harvested in the same batch, the higher the TSS, lower TA, and the higher the TSS/TA ratio, while the acetaldehyde (AA) and ethanol content are similar at each maturity in the harvest. In the last fruit harvested, the TSS and TA were less. The TSS/TA ratio increased initially and then declined with maturity. Higher levels of AA and ethanol are found in late-harvest fruit during cold storage and in modified atmosphere packaging (MAP). Fruit harvested late are also likely to show higher levels of decay after cold storage. H. Wang et al. (2003) found that late in Feizixiao fruit development, the sugar translocation to the fruit declined and stopped, and the already accumulated sugar is diluted by the water uptake, which continued, resulting in the phenomenon called "sugar withdrawal." The conclusion is that leaving ripe fruit on the tree during harvest season often leads to more rapid loss in quality and marketable fruit after shipping, storage, and retailing.

4.1.2 | Changes in sugar and acidity in the aril

Sucrose, glucose, and fructose are the main sugars with the amount and ratio differing between cultivars which is highly related to the activities of enzymes including acid invertase (AI) and SS as discussed above (Paull et al., 1984; H. Wang et al., 2003, 2006; Z. Yang et al., 2013). The composition of sugar might affect the accumulation of sugar. Nuomici, a sucrose prevalent type, accumulates more sugar than Feizixiao, a reducing sugar prevalent type, which might contribute to the osmotic pressure with disaccharides being only half that of monosaccharides. The compartmentalization of sugars into the vacuole through sugar pumps is critical to maintaining an osmotic pressure gradient and continued sugar accumulation. These data also suggest that the unloading of sugar in the fruit is dependent on cell wall invertase (CWI), thereby maintaining the sucrose concentration gradient in the phloem (H. Wang et al., 2003).

The abscisic acid concentration of aril and pericarp increases as the fruit matures (H. Wang et al., 2007). Transfusion into exogenous abscisic acid (ABA) 3 weeks before harvest accelerates sugar accumulation and pericarp pigmentation with no effect on chlorophyll degradation, whereas 6-benzyl aminopurine (6-BA) limited these changes. The results suggested that 6-BA reduced ABA levels. Aril 1-aminocyclopropane-carboxylic acid (ACC) and 1-aminocyclopropane-carboxylic acid oxidase (ACO) activities change little during sugar accumulation. Infusion of aminooxy acetic acid caused a significant decrease in ACC concentration without an effect on sugar accumulation in aril. ABA is potentially critical for the synthesis of pericarp anthocyanins and aril sugar accumulation, while ethylene is involved in the breakdown of pericarp chlorophyll (H. Wang et al., 2007).

During the maturation of the fruit, the aril pH decreases from 3.18 to 2.68 during fruit growth and then increases to 4.49 during ripening. This change in pH correlates with a decrease in TA from 4.44% to a final value of 0.16% (Rivera-López et al., 1999). The decrease in pH and acidity (Figure 2a) parallels the decline in the content of aril malic acid (Figure 2b). Malic is the major organic acid present in aril with small amounts of tartaric, citric, and ascorbic acid (AsA). The AsA concentration decreases during fruit growth until 2 weeks before harvest when it increases slightly as the fruit begins to ripen. AsA levels varied widely among the eight cultivars evaluated by H. C. Wang et al. (2006). Monosaccharide-prevalent cultivars contained more AsA than disaccharide-prevailing types.

4.1.3 | Structure of the pericarp

The litchi leathery tuberculate pericarp begins to differentiate with the formation of the pericarp (epicarp, mesocarp, and endocarp) and completely lacks functional stomata when mature. When ripe, the leathery texture of the pericarp is due to brachisclereides (stone cells) found immediately below the epidermis. The function of brachisclereides may be to protect against mechanical and physiological stresses and herbivores (Nacif et al., 2001). Underhill and Critchley (1992) found that the pericarp was initially folded, with subsequent growth and expansion driven by aril development. A "Zig-zag unfolding" model for pericarp extension driven by expanding aril has been proposed (X. M. Huang et al., 2004). The thickness decreased as the fruit approached maturity, being 400–500 μm thick at maturity (Riederer et al., 2015). Microcracking of the pericarp is observed 62 days after anthesis (Underhill & Critchley, 1992), although Sivakumar and Korsten (2005) reported microcracking much earlier 20 days after the initial fruit set.

The variety and the structure of the pericarp affect the extent of cracking of the fruit. Huaizhi is a crack-resistant cultivar, with a cracking rate of <6%, while Nuomici is a cracking-susceptible cultivar, with a cracking rate of >34% (X. M. Huang et al., 1999). Huaizhi pericarp has a higher mechanical and tensile strength, and extensibility, and, therefore a greater threshold-cracking turgor pressure. The Huaizhi pericarp has a higher calcium content and cell wall structural components (cellulose, hemicellulose, and insoluble pectin) that could contribute to its higher pericarp strength and thus cracking resistance compared with Nuomici. The higher pericarp strength and extensibility in Huaizhi than in Nuomici

before rapid expansion allowed for greater flexibility during growth. Huaizhi also has a thicker spongy mesocarp tissue than Nuomici, which could also allow greater pericarp extensibility.

The thickness may also contribute to resistance to cracking, water loss, and browning of the pericarp. Treatment of fruit with cytokinin (CK) at the stage of division of the pericarp cell wall led to mature fruit with thicker pericarps, a reduced rate of postharvest water loss, and reduced susceptibility to postharvest pericarp browning (Fahima et al., 2019). This difference is associated with increased cell proliferation in the parenchymatic tissue and the highly lignified brachysclereid cell layer. Later treatments with exogenous CK, following the phase of pericarp cell division, significantly increased epidermal-cell proliferation but had no significant effect on the overall fruit pericarp thickness and only a minor impact on postharvest water loss and browning of the pericarp.

Litchi has a unique cuticle structure with both endocarp and exocarp cuticles and a fleshy mesocarp that is a few cells thick. Epidermal cells have a thick arch-shaped cuticle. The endocarp cuticle is thinner (Riederer et al., 2015). The main function of these cuticles is to provide resistance to water loss. Cuticle accumulation occurred on the entire epidermal surface from an early stage of fruit development. The layers are parallel to each other in the early stages and become more wrinkled, compact, and protruding as the fruit matures (Sivakumar & Korsten, 2005). Riederer et al. (2015) found a significant number of very long-chain aliphatic (>C18) and cyclic compounds on the surfaces of endocarp as well as exocarp. These constituents are common to plant cuticular waxes. This double cuticle serves as two transpiration barriers: the exocarp cuticle controls water loss from fresh fruit, while both barriers are involved in harvesting fruit held at lower humilities. The barrier characteristics of the litchi cuticle are similar to those reported for other fruit cuticles (Riederer et al., 2015).

4.1.4 | Compositions of pericarp pigments

The composition of the pigments of litchi pericarp contains chlorophyll, anthocyanin, phenols, and flavonoid (Z. Q. Hu, Huang, et al., 2010; Lee & Wicker, 1991a; Paull et al., 1984; Reichel et al., 2011). Anthocyanins are the components that produce red in the pericarp and decline with storage or browning of the pericarp (D. Zhang et al., 2000; Z. Zhang et al., 2001). In the pericarp of Brewster, cyanidin-3-rutinoside is the major anthocyanin, with cyanidin-3-glucoside and malvidin-3-acetylglucoside are also found (Lee & Wicker, 1991a). In other cultivars Kwai Mi (Guiwei), Huaizhi, and Kom, cyanidin-3-rutinoside (>90%) is also the main component, with smaller amounts of cyanidin glucoside, quercetin-3-rutinoside (rutin), and quercetin glucoside (Ducamp-Collin et al., 2008; Sarni-Manchado et al., 2000; Somboonkaew & Terry, 2010; Z. Zhang et al., 2004). For Calcuttia cultivar, the cyanidin-3-O rutinoside content was more variable being 71%–96% of total anthocyanins (S. P. Singh et al., 2014).

Condensed tannins (4 mg g^{-1} of fresh pericarp) are the main phenolic in cultivar Kwai Mi (Guiwei), with smaller amounts of (-)-epicatechin and procyanidin A2 (1.7 and 0.7 mg g^{-1} FW, respectively). The content of pericarp anthocyanins is similar to that of flavonols (0.4 mg g^{-1} FW) (Sarni-Manchado et al., 2000). In Huaizhi, flavan-3-ol monomers and dimers are the most common phenolic compounds, 87% of the total phenolics with the amount decreasing during storage and browning (D. Zhang et al., 2000). The (-)-epicatechin content tends to decline during fruit development. Nuomici has more total phenolics and (-)-epicatechin than Feizixiao (J. Sun et al., 2009). Although (-)-epicatechin and A-type procyanidins are present in greater amounts in Hong Huey and Chacapat, (-)-epicatechin has stronger antioxidant activity than procyanidin A2 based on its reducing power and scavenging activities of the DPPH radical, and the hydroxyl and superoxide radicals (J. Sun, Jiang, et al., 2010). Minor novel flavonoids such as monohydroxylated structures (Reichel et al., 2011), procyanidin A2, procyanidin B2, and quercetin-3-O-rutinoside-7-O-α-L-rhamnosidase are detected in the pericarp (Deng et al., 2018). The bound phenolic in the pericarp increases during storage, while the free phenolic initially increases and then decreases (M. X. Wu et al., 2001).

Total phenolics in dried litchi pericarp vary considerably from 51 to 102 g kg^{-1} in 10 cultivars tested (H. C. Wang et al., 2011). Nuomici had higher total soluble phenolics made up of proanthocyanidins, flavonoids, and phenolic acids than the other cultivars, with Lanzhu and Guiwei having the least total phenolics. These litchi pericarp phenolics, flavonoids, and proanthocyanidins are highly oxidizable due to their ortho-diphenolic structure (Sarni-Manchado et al., 2000). Antiradical activities of these compounds are positively correlated with phenolic content in eight cultivars (Z. Q. Hu, Huang, et al., 2010). There is no relationship between lipid oxidation and phenol content. For example, Feizixiao has a high phenolic content and radical scavenging rate but limited lipid oxidation. Pericarp anthocyanins also strongly inhibit linoleic acid oxidation and deoxyribose degradation by acting as iron ions rather than directly scavenging hydroxyl radicals (Duan et al., 2007). Nuomizi has the highest total phenolic content and the strongest DPPH radical scavenging activity (Zhong et al., 2008). However, the extraction method can influence the results, and care is needed in interpretation. Pericarp extracts have higher FRAP and strong DPPH scavenger activity, lipid peroxidation inhibition, and protection from oxidative DNA damage. Among the cultivars tested, concentrations of major phenolics had significant linear correlations with FRAP and DPPH scavenging activities

(Z. Q. Hu, Huang, et al., 2010). Phenolic content increases and decreases in adenosine triphosphate (ATP)-treated and dinitrophenol (DNP)-treated litchi fruit, respectively. The increase in the content of phenolic compounds increases DPPH scavenging ability, with correlation coefficients of $r^2 = 0.63$ (Yi et al., 2010). Among the three cultivars tested, Jingganghongnuo showed the slowest changes in the browning indices and had the highest content of epigallocatechin, (-)-epicatechin, epicatechin gallate, gallocatechin gallate, procyanidin A2, total phenols, and anthocyanins (Tang et al., 2020).

The anthocyanins applied to harvested litchi fruit significantly reduced the browning of the pericarp and delayed the increase in the permeability of the membrane (Duan et al., 2007). Extracted anthocyanins are unstable, and temperature and pH affect antioxidant ability (Ruenroengklin et al., 2008). Heat treatment for 30 min at 45˚C has the greatest antioxidant effect, with the highest total antioxidant capacity and the scavenging activity of DPPH radicals at pH 3–5. Deng et al. (2018) found that low-temperature storage of fruit preserved more phenolics and retained higher antioxidant activity than storage at room temperature. Total phenolic and procyanidin contents of the pericarp decrease by 20% and 24% at 4˚C after 7 days and 37.8% and 47.8% at 27˚C for 3 days, respectively. The oxygen radical absorbance capacity and the cellular antioxidant activity under these same storage conditions decreased by 17.6% and 58.7% at 4˚C and 23.4% and 66.0% at 7˚C, respectively.

Another component of the colour of the pericarp is chlorophyll that begins to decline soon after the start of the fruit growth, with anthocyanin synthesis beginning when the fruit is about half-grown (B. Lai et al., 2015; Paull et al., 1984). The color of the pericarp changes from light green to yellow green (12–15 weeks after anthesis) and then yellow-red to dark red during fruit development. In the later fruit development stages, chlorophyll degradation and flavonoid production occurred simultaneously (Underhill & Critchley, 1992). Increases in both monomeric anthocyanins and total Acy levels occur with green fruit containing malvidin-3-acetylglucoside and polymeric pigment. The raw fruit as indicated above has cyanidin-3-rutinoside (>75%), cyanidin-3-glucoside (<17%), and malvidin-3-acetylglucoside (<9%) (Rivera-López et al., 1999). The biggest change in color occurs in the last 15–20 days when the chlorophyll decreases by 73%–92%, and there is a 7- to 38-fold increase in anthocyanin (Reichel et al., 2011). In fresh tissue, the anthocyanin pigments are restricted to the mid-to-upper mesocarp and epicarp region, with the epicarp content being much greater than the mesocarp (Underhill & Critchley, 1993a, 1993b). Cultivars differ in depth of the red hue. Huaizhi contained more anthocyanins and has a darker red hue (higher CIE a^* value) than Guiwei. After postharvest treatment with citric acid treatment and cold storage, Huaizhi had less anthocyanin remaining than Guiwei and a lower CIE a^* value (Ducamp-Collin et al., 2008).

ABA may play a role in the reddening of the pericarp during fruit maturation. The ABA content in pericarp and aril increases about 62 days after anthesis and parallels the increase in pericarp anthocyanin and aril sugars (H. C. Wang et al., 2001). The application of ABA promotes anthocyanin synthesis with only minimal effect on chlorophyll degradation. Treatment of fruit with BA retards the increase in both anthocyanin and ABA, without changing the ACC content. Treatment with ethephon increases ACC content of ACC, although it does not have an effect at lower concentrations (400 mg L^{-1}) in the increase in pericarp anthocyanin, but higher concentration (800 mg L^{-1}) increases the rate of chlorophyll degradation and anthocyanin synthesis. A combined treatment of ethephon at the lower concentration with ABA increased both chlorophyll degradation and anthocyanin synthesis. The results suggest that ABA plays a role in fruit maturation, suggesting that ABA appears to be more closely associated with ethylene in fruit maturation. The authors suggest a synergistic action between ethylene and ABA in the development of pericarp colour, with ABA being crucial for anthocyanin synthesis and increases the sensitivity of the pericarp to ethylene with ethylene leading to chlorophyll degradation (H. Wang et al., 2007). This is supported by the application of ABA in the color-break stage increasing the concentration of total anthocyanins and cyanidin-3-O-rutinoside with no significant effect on the concentrations of (-)-epicatechin and quercetin-3-O-rutinoside (S. P. Singh et al., 2014). Yin et al. (2001) had previously reported that litchi fruit treated with silver thiosulphate (STS), an inhibitor of ethylene synthesis, exhibited a green-to-yellow colour with higher chlorophyll content and lower anthocyanin content compared with the red of the control.

Other plant growth regulators can change the accumulation of maturation-associated anthocyanin, and chlorophyll degradation can also be delayed by CK treatment 4 weeks after the full female bloom during the pericarp cell division phase (Fahima et al., 2019). The highly active cytokinin-like plant growth regulator 1-(2-chloropyridin-4-yl)-3-phenylurea (CPPU) applied to green or color-broadening Mauritus fruit delays harvesting by 2–3 weeks (A. R. Stern et al., 2006). At harvest, these CPPU-treated fruit did achieve a red hue similar to the earlier harvested control fruit and, more importantly, are 20%–25% larger in size with a TSS/TA ratio that is 50% higher than the controls, suggesting a longer growth period to increase in size and sugar accumulation. The CPPU-treated fruit could also be stored for 6 weeks at 1˚C with reduced browning, lower decay development, less aril discoloration, and an acceptable flavor.

The absence of anthocyanins in immature litchi and CPPU-treated fruit is associated with the absence of UDP-glucose: flavonoid 3-O-glucosyltransferase (UFGT) expression

(Wei et al., 2011). UFGT shows de novo gene expression when fruit are exposed to light, and this is correlated with anthocyanin biosynthesis ($r = 0.84$). This new expression of UDP-glucose: flavonoid 3-O-glucosyl transferase (UFGT) is enhanced by ABA treatment. This result follows from the earlier report (B. Lai et al., 2014) that ABA and light promoted the LcMYB1 transcription factor, whereas CPPU and bagging inhibited expression and anthocyanin accumulation. The cis promoter motifs of LcMYB1 include light and abscisic acid responsiveness. Exogenous application of ABA leads to an upregulation of genes involved in flavonoid and anthocyanin biosynthesis (B. Hu et al., 2018). Included in the upregulated genes are phenylalanine ammonia lyase (PAL), C4H, chalcone synthase (CHS), chalcone isomerase (CHI), dihydroflavonol 4-reductase (DFR), LDOX, and GTs. CPPU induces genes associated with carbon metabolism, amino acid biosynthesis, and photosynthesis and downregulation of genes related to anthocyanin biosynthesis. There is also increased expression of chlorophyll synthesis genes and inhibition of the chlorophyll degradation gene (SGR). This antagonistic interplay of ABA and CK also spills over the expression of genes involved in the auxin, GA, and ethylene signaling pathways. The conclusion is that there is a complex network of genes involved in the regulation anthocyanin biosynthesis and chlorophyll degradation.

Genes that encode the enzymes involved in chlorophyll degradation and flavonoid biosynthesis have been identified in the pericarp transcriptome. The stay-green (SGR) protein is suggested to play a key role in chlorophyll degradation. The expression levels of most genes involved in late anthocyanin biosynthesis are upregulated and coincident with the accumulation of anthocyanins. Genes involved in light-induced anthocyanin biosynthesis are rapidly induced when bunches of fruit previously held in black bags for 42 days were exposed to light. The anthocyanin biosynthesis genes UFGT, MYB, basic helix-loop-helix protein (bHLH), and WD40 are all rapidly upregulated in expression (H. N. Zhang et al., 2016). Expression in the pericarp of LcF3H, LcDFR, LcANS, and LcUFGT, in the pericarp of non-red cultivars, is much lower than in full red Noumici. The expression of the genes, LcDFR and LcUFGT, correlate with the pericarp anthocyanin concentrations, suggesting coordinated expression during the reddening of the pericarp (Wei et al., 2011).

MYB transcription factors have been implicated in the regulation of flavonoid biosynthesis (B. Lai et al., 2015). LcMYB1 is only detected in tissues and is positively correlated with the content of pericarp anthocyanin in the 12 genotypes evaluated. LcUFGT is the only structural gene that is highly correlated with LcMYB1, suggesting that LcMYB1 controls anthocyanin biosynthesis by regulating and targeting LcUFGT. A protein complex of MYB-bHLH-WD40 is required to activate biosynthetic genes. There are three litchi bHLH candidate anthocyanin regulators: LcbHLH1, LcbHLH2, and LcbHLH3. Only LcbHLH1 and LcbHLH3 are found in the nucleus and interact with LcMYB1. When LcMYB1 and both LcbHLH1 and LcbHLH3 are co-infiltrated in tobacco leaves, there is enhanced anthocyanin accumulation, with LcbHLH3 being the best inducer. Both LcbHLH1 and LcbHLH3 are critical for LcMYB1 in the regulation of the production of anthocyanin synthesis in tobacco systems and potentially also in litchi. This LcMYB1-LcbHLH complex may activate the transcription of dihydroflavonol-4-reductase (DFR) and anthocyanidin synthase (B. Lai et al., 2016). LcMYB5 and a new R2R3-MYB from the litchi transcriptome may also be involved (B. Lai et al., 2019) in regulation even though LcMYB5 is not correlated with tissue colouration. The overexpression of LcMYB5 in tobacco and petunia results in enhanced anthocyanin biosynthesis along with the upregulation of their endogenous bHLHs and key structural genes such as DFR.

The anthocyanin synthesis pathway may also be controlled by small RNA (siRNA). miR156a and a new microRNA (NEW41) are differentially expressed during fruit ripening (R. Liu et al., 2017). The target genes (LcSPL1/2, LcCHI) for these miRNAs are inversely expressed during anthocyanin synthesis. The miR156a target gene (LcSPL1/2) are transcription factors that are located in the nucleus. The LcSPL1 proteins can potentially interact with LcMYB1, the key regulatory gene in litchi anthocyanin biosynthesis.

The complexity of pericarp browning is highlighted by a metabolomics study in four litchi cultivars (X. Chen et al., 2019). Thirty primary metabolites, 44 volatile compounds, 29 free amino acids, and 16 hydrolytic amino acids are detected. Feizixiao, a cultivar less susceptible to pericarp browning, had a much higher content of many amino acids that could influence the browning rate. In three other cultivars, more prone to browning, they had more soluble sugars and some free amino acids that are negatively correlated with the browning rate. Sesquiterpenes are also induced and may positively be related to browning. The amino acid content is negatively correlated with volatile compounds. The authors of this study proposed that amino acids were being converted to terpenes (X. Chen et al., 2019), although this would require the amino acids to be funneled as primary substrates into terpene biosynthesis as C5-unit isopentenyl diphosphate (IPP) and its isomer dimethylallyl diphosphate (DMAPP) (Tholl, 2006).

4.2 | Postharvest physiology

4.2.1 | Respiration

The respiration rate of litchi fruit declines throughout their development (J. Jiang et al., 1986) and declines further after harvest (J. Jiang et al., 1986; Paull & Chen, 1987; Reichel et al., 2010). The respiration of green fruit is higher than that

of mature fruit (J. Jiang et al., 1986). The respiration rate is in the range of 25–40 mL of CO_2 kg^{-1} h^{-1} (Paull et al., 1984) and gradually decreases from 30–50 mL to 25–35 mL CO_2 kg^{-1} h^{-1} at 20°C for 7 or 13 days, respectively (Tongdee et al., 1982). Over this period, the fruit turns from red to brown, indicating that the respiration rate is not affected by pericarp browning.

At 5°C, the respiration rate is significantly lower but increases rapidly when transferred to 25°C (J. Jiang et al., 1986). Ethylene treatment does slightly increase respiratory rate and does not affect pericarp browning (Pang et al., 2001c). When stored at 95% RH, the respiration rate is lower along with water loss and pericarp browning (Xiao et al., 2019). Latent anthracnose infection does increase the respiration rate (A. Liu et al., 2005). Polyphenol treatment can also reduce the respiration rate and weight loss in litchi fruit during storage (Z. Su et al., 2019). Sulfur fumigation leads to a lower respiration rate, while desulfurization led to a recovery of the respiration rate (Luo et al., 2019). A hot water treatment (70°C, 20 s) greatly reduced respiration rate, which is further reduced by acid dipping (Fang et al., 2013).

4.2.2 | Ethylene

The ethylene production of litchi fruit declines throughout their growth and development (J. Jiang et al., 1986; H. Wang et al., 2007). A transient increase in endogenous ethylene production is detected near the color break stage in Nuomici, though the cause is unclear (H. Wang et al., 2007). Interestingly, enhanced ACO activity is detected in the pericarp at the same stage.

Overall, the reported ethylene production is very low (0.9 μL kg^{-1} h^{-1}) at harvest, decreasing to about 0.1 μL kg^{-1} h^{-1} in 2 days (Underhill & Critchley, 1993b), or less than the detection limit ~1 nL kg^{-1} h^{-1} (Paull et al., 1984, 1987; Paull & Chen, 1987). However, Tongdee et al. (1982) found the ethylene production rate for five cultivars increased gradually from 0–0.1 μL kg^{-1} h^{-1}, right after harvest, to 0.3–0.5 μL kg^{-1} h^{-1}, several days after harvest. Similarly, Y. M. Jiang and Chen (1995) also found that ethylene production increases from 57 nL kg^{-1} h^{-1}, right after harvest, to 203 nL kg^{-1} h^{-1} 30 days at 5°C after harvest.

The ethylene produced by the pericarp of mature litchi fruit is 86 times that of aril and seed on a fresh weight basis (J. Jiang et al., 1986). The authors also found that internal ethylene peaked at 17.6 ppm. Polyamine treatment can reduce ethylene production (Y. M. Jiang & Chen, 1995), while ethylene production is enhanced by anthracnose infection (A. Liu et al., 2005). The three polyamines (putrescine, spermidine, and spermine) decrease in the pericarp during browning as the ethylene production increases. Treatment of litchi with these polyamines individually led to an increase in the other two polyamines and delayed senescence changes that included browning, peroxide level, ethylene production, and cell leakage (Y. M. Jiang & Chen, 1995).

High ethylene production by the pericarp in mature fruit (J. Jiang et al., 1986) and ethephon and ABA treatment are associated with accelerated chlorophyll degradation and anthocyanin synthesis during fruit maturation (H. Wang et al., 2007). This application of mature ethephon fruit also led to an increase in pericarp chlorophyll degradation but did not impact anthocyanin synthesis (S. P. Singh et al., 2014). Ethylene treatment does increase pericarp PPO and POD activity (J. Jiang et al., 1986; Pang et al., 2001c), although this does not substantially affect pericarp browning (Pang et al., 2001c; S. P. Singh et al., 2014). This observation is supported by 1-methylcyclopropene (1-MCP) treatments that do not significantly affect PPO and POD activity, respiratory rate, ethylene production, or the chemical composition of litchi fruit (Pang et al., 2001c). The results imply that the browning of postharvest litchi fruit is not directly affected by ethylene.

Ethylene can lead to early aril deterioration (Kader, 1998). This aril deterioration is associated with softening and loss of acidity (S. P. Singh et al., 2014) with no effect on soluble solids. This has been confirmed by Pang et al. (2001c) who found that treatment with ethephon or 1-MCP does not affect the TSS, TC, and vitamin C of fruit storage at 23–25°C for 10 days.

4.2.3 | Changes in aril during fruit senescence

Delaying the harvesting of mature red fruit and prolonged storage has often been associated with aril breakdown (softening, loss of turgidity, and translucency) and having a bland flavor (Holcroft et al., 2005; Kader, 1998; Paull et al., 2014). The deterioration begins at the end and spreading back to the end of the stem. This loss in aril flavor has been associated with a decrease in malic acid and a hence TA and loss of sucrose with changes in glucose and fructose levels. Storage at 2°C reduces the rate and extent of changes (Paull & Chen, 1987). There is potentially an involvement of invertases, as Somboonkaew and Terry (2010) showed that storage for 9 days at 13°C increased fructose and glucose and decreased sucrose. These sugar changes during storage are not affected by being kept at 80% RH or 100% RH. The rate of decline in aril quality traits (TA, TSS, total soluble sugars, and vitamin C) at 25°C is rapid (X. Jiang et al., 2018). In late harvested fruit, both acetaldehyde and ethanol have also been shown to increase during cold storage and MAP (Pesis et al., 2002) and could be expected to increase under other storage regimes.

MAP and wrapping have been shown to delay browning and maintain fruit quality. The storage of wrapped fruit for 18 days

at 5°C is 100% marketable, while only 17% of the unwrapped fruit was sellable (Vilasachandran & Sargent, 1997). The wrapped fruit had reduced weight loss, higher moisture content and aril TA, and lower aril pH. Removing the fruit from the panicle and sale as individual fruit in a punnet or wrapped reduced weight loss with the fruit still attached to the panicle lost 3% weight loss. The fruit attached to the panicle tended to show a decline in TA and an increase in pH.

Coating and other treatments can significantly alter the quality changes during storage. Chitosan coating (X. Jiang et al., 2018), or treatment with apple polyphenols (Z. Su et al., 2019), maintained aril sucrose levels while slowing the decrease in glucose and fructose content. Treatment with apple polyphenols led to the aril having higher levels of all organic acids, phenolic compounds, ascorbic acid, and glutathione. These higher levels potentially contributed to the maintenance of quality and nutritional. Furthermore, aril shows improved antioxidant capacity, with radicle scavenging due to higher DPPH and FRAP.

Proteomic analysis has implicated auxin and ethylene in aril senescence, with genes being upregulated in a coordinated fashion that are implicated in increased fruit softening, deterioration, and senescence (T. Li et al., 2015). Reactive oxygen species (ROS) scavenging, glycolysis, and tricarboxylic acid cycle metabolism, and downregulation of ATP synthesis are possibly associated with histone deacetylase and DNA methyltransferase activity. More differentially expressed proteins are upregulated during aril senescence and include several metabolic processes such as cell wall biosynthesis and turnover, anaerobic respiration, and protein and lipid turnover. These proteomic results are supported by the downregulated methionine (Met) sulfoxide reductase gene that plays a crucial role in the repair of oxidized Met residues in litchi calmodulin (LcCaM1) (G. Jiang et al., 2017). The oxidation of Met residues caused by ROS in LcCaM1, a substrate of LcMsrA1/B1, could be important in aril senescence. This Met oxidation in LcCaM1 increases the binding of two senescence-related transcription factors LcNAC13 and LcWRKY1 to DNA and leads to aril senescence.

4.2.4 | Pericarp browning

Influence and character of pericarp browning

The browning of litchi pericarp is the major cause of loss in fruit appeal and limits marketing and consumer acceptability (Akamine, 1960; Holcroft & Mitcham, 1996; Y. M. Jiang et al., 2006; Sivakumar et al., 2010). As indicated above, this process is very rapid with 50% of the pericarp turning brown within 12 h after harvest at room temperature (Underhill & Critchley, 1993b). The fruit turns completely brown within 24–48 h after harvest (Pang et al., 2001b; Reichel et al., 2013; Underhill, Simons, et al., 1992; J. P. Zhang et al., 2014). Fruit are regarded by some as unsaleable in 3 days or less unless refrigerated and packaged (Campbell, 1959), though the pericarp browning has little effect on aril quality parameters (sugar, acids, and phenol) (Paull & Chen, 1987).

Initially browning is first observed on the tips, pericarp protuberance apices and then extends over the entire surface (Campbell, 1959; Underhill & Critchley, 1995). These pericarp protuberances are easily damaged by fruit rubbing other fruit before harvest and each other and storage surfaces after harvest. Holding fruit at ambient and high temperatures leads to uniform browning of the surface (Underhill & Critchley, 1994). Reichel et al. (2013) described two types of browning in packaged litchi after 52 days of storage at 5°C. The fruit located in the center of the basket is dark brownish-red, and the fruit on the outside is light brown. The difference in color is most likely due to the different vapor pressure gradients, and hence water loss rate with a higher rate from the fruit on the outside than those on the inside of the package.

Browning at the tissue level is localized and can be seen when the fruit are held at 25°C and 60% RH (Underhill & Critchley, 1995) initially localized to the epicarp and the upper mesocarp. Anthocyanins are in the upper mesocarp parenchyma (Underhill & Critchley, 1993b) and during storage are lost, and the mesocarp becomes progressively colorless (Underhill & Critchley, 1994). Browning of the tissue can be induced in 2 min after heating at 60°C for 10 min. The progression of browning is similar after heat treatment and under ambient desiccation conditions, although the brown pigmentation distribution is distinct (Underhill & Critchley, 1993a). Heat treatment leads to a uniform distribution of browning in the pericarp. While ambient desiccation induces highly localized browning suggesting more extensive pericarp phytotoxicity by heat treatment that may result from nonselective degradation of a range of compounds, including anthocyanin. This heat induced progressive browning from the epicarp inwards being associated with dehydration and different compounds.

Anthocyanins decline during the pericarp browning from 1.77 to 0.73 mg g^{-1} on a fresh weight basis (Lee & Wicker, 1991b). This decline occurs in three anthocyanins: cyanidin-3-glucoside, cyanidin-3-rutinoside, and malvidin-3-acetyl-glucoside. The decrease in anthocyanins is concomitant with the gradual increase in polymeric pigments from 20.9% to 53% during browning. The authors suggested that the anthocyanins initially responsible for litchi pericarp color are replaced by more stable polymeric pigments. Other authors have suggested that there is no clear relationship between litchi pericarp browning and anthocyanin degradation (Underhill & Critchley, 1993b) with anthocyanin degradation occurring slower than tissue browning. Z. Zhang et al. (2001) found differences with the litchi pericarp browning index increasing, while the content of anthocyanins decreased. The two groups used different anthocyanin

extraction solutions 0.1 M HCl (Z. Zhang et al., 2001) versus acidic methanol (Underhill & Critchley, 1993b). Acidic methanol is also expected to also extract water-insoluble brown compounds and interfere with the determination of anthocyanin. The result with I M HCL shows a significant inverse relationship between anthocyanin content and pericarp browning (Z. Zhang et al., 2001, 2002; Z. Q. Zhang et al., 2003).

Considerable effort has been made to understand the phenolic oxidation associated with pericarp browning. Litchi PPO has been implicated, as the addition of litchi PPO to a phenolic extract turns dark brown rapidly. The absorbance at 410 nm increases during this oxidation and is correlated with epicarp browning (Y. Jiang, 2000). A lipofuscin-like (lipid-associated yellow granules) material is the result of oxidation of cellular membranes and contents via lipid hydroperoxides, malondialdehyde, and protein oxidation. Similar changes during senescence are also reported in pericarp browning (S. Yang et al., 2011). During storage of 72–144 h, the relative content of the lipofuscin-like substance increased by 51%, while (-)-epicatechin decreased by 41% and anthocyanins by 98%. There was a parallel increase in both lipofuscin-like material and browning index. These yellow granules could be one of the final products of this oxidative process.

More focus has been placed on the roles of phenolics and PPOs in pericarp browning. Litchi pericarps are rich in both phenols and anthocyanins. PPO accepts both monophenols and diphenols as substrates and catalyzes the oxidation of o-diphenols to o-quinones. o-Quinones can then be rapidly polymerized by PPO to produce polyphenols that range from black to brown or red pigments, and are detected in pericarp browning (Anon, 2022; Y. Jiang, 2000; Z. F. Lin, Li, Lin, et al., 1988; Tan & Li, 1984). PPO does not directly oxidize anthocyanins but can degrade anthocyanin in the presence of (-)-epicatechin and catechol to produce a brown pigment (Y. Jiang, 2000; Ruenroengklin, Sun, et al., 2009). The products of the hydrolysis of anthocyanin by ANT can then be oxidized by PPO, resulting in brown pigment and browning of the pericarp (Z. Zhang et al., 2001).

Factor affecting pericarp browning

Many factors can lead to or accelerate pericarp browning, including water loss, senescence, chilling, physical injury, and disease.

Water loss. Water loss has always been considered a major factor leading to the browning of the litchi pericarp. Correlation, stepwise regression, and path analyses have highlighted the role of pericarp water loss in browning (J. Wang, Wang, et al., 2010; Xiao et al., 2019). When litchi fruit are stored in different temperatures and relative humidity regimes, the degree of pericarp browning with the degree of tissue browning is proportional to the rate of pericarp desiccation (Underhill & Critchley, 1993b, 1994). As the storage relative humidity was reduced from 90% to 60% RH and thus the vapor pressure deficit increased, pericarp browning increased (Y. M. Jiang & Fu, 1999a). Initially, this appears as brown spots on a bright red pericarp and around the pericarp protuberances that enlarge and coalesce under very low RH condition or prolonged exposure until the surface is completely brown (Paull et al., 2014). Packaging in perforated polyethylene bags slows the rate of water loss and the rate of browning (Campbell, 1959). Under these conditions of near 100% RH in a plastic bag, fruit can be 100% marketable after 18 days of storage at 5˚C. Unwrapped fruit held at 84% RH is only 17% marketable (Vilasachandran & Sargent, 1997). Xiao et al. (2019) stored litchi fruit in a humidified room at 95% RH, and the fruit had slight weight loss and no obvious pericarp browning, without humidity control, underwent rapid weight loss, accompanied by severe pericarp browning after 25 days at 4˚C. Coatings that include organic acids (citric or tartaric) with chitosan, at a pH of 0.8, 1.0, and 1.3, showed that the browning rate parallels the dehydration rate and the pH of the pericarp during storage (Joas et al., 2005).

Water loss shows a biphasic state with an initial rapid loss followed by a transition to a slower equilibrium rate (Riederer et al., 2015). The transition occurs in fruit at 25˚C and 0% HR after about 20 h. The difference in water loss rate between initial and equilibrium is much higher at 0% RH than that at 80% RH. This loss pattern is due to the unique transpiration pathway consisting of two resistance barriers described earlier: endo and exocarp cuticles. The two barriers create two "fleshy" compartments (water reservoirs): the pericarp mesocarp and the fleshy aril. The exocarp cuticle controls the initial water loss from the pericarp, especially the mesocarp with a fast water loss rate and increases the resistance pathway length, while in the slow equilibrium rate of water loss is controlled by the dried exocarp and its cuticle, the dried mesocarp and the endocarp cuticle controlling the water loss from aril. This difference in the rate of water loss from different tissues had been reported earlier, whereas 24 h from harvest the total loss of fruit weight is 8%, while the pericarp lost 43% of its weight (Underhill & Simons, 1993) with similar results reported elsewhere (Bryant, 2012; X. M. Huang et al., 2005). The initial high rate of water loss is associated with the pericarp and later slower equilibrium rate with the aril and seed once the pericarp has completely desiccated, giving rise to the biphasic pattern with the changeover occurring 24–72 h after harvest depending on the storage RH (Riederer et al., 2015; Underhill & Simons, 1993; J. Wang, Wang, et al., 2010). The leakage of the pericarp membrane becomes very high 2 days after harvest, while that of the aril remains intact (X. M. Huang et al., 2005).

The nature and structure of the cuticle layer do impact water loss rate, though the focus has been on the cuticle coating the exocarp. There are differences between the cuticles on

different cultivars. The water loss rate from Nuomici is almost double that of Huaizhi (X. M. Huang et al., 2004). Huaizhi has a cuticle throughout the exocarp from very early stage in development, while Nuomici cuticle is more localized. Furthermore, during fruit development, the cuticle thickness declines from 8.75 to 1.88 μm (Underhill & Critchley, 1992). However, after harvest, the thickness of the pericarp decreases from 1.2 to 0.4 mm during an 8-day storage period at 5°C, 90% RH (Reichel et al., 2013). As discussed above, the thickness of the pericarp can be increased by CK treatment during the pericarp cell division phase; later application showed no increase. Thicker pericarp meant reduced rate of postharvest weight loss and reduced pericarp browning (Fahima et al., 2019).

Pericarp microcracking is observed with 1–2 months after anthesis and may influence water loss rate after harvest (Sivakumar & Korsten, 2005; Underhill & Critchley, 1992) and in mature fruit (Sivakumar & Korsten, 2004; Underhill & Simons, 1993). These microscopic cracks (20–100 μm wide) on the surface observed on harvested fruit increased within 12 h, and the cracks extend through the sub-epidermal sclerenchyma layer into the mesocarp. The microcracks have been associated with desiccation and exposure of mesocarp anthocyanin (Underhill & Critchley, 1993b; Underhill & Simons, 1993), though pericarp desiccation occurs prior to this expanding of cracking and maybe an effect rather than a cause of increase water loss. The data do not yet resolve whether the high initial rate of water loss can be attributed to cuticle water vapor permeability, cuticle or pericarp damage, or the presence of lenticles. Rough handling during harvesting and packing contributed to more microcracking (Sivakumar & Korsten, 2004). Microcracks can occur by exposing the anthocyanin-containing mesocarp to a higher rate of desiccation and possibly fungal penetration (Underhill & Simons, 1993). Surface scuffing or pericarp abrasion can increase the rate of water loss (Reichel et al., 2013).

Factors that change the vapor pressure gradients from the surface of the fruit to ambient environment affect the loss of water. Low temperature and high RH can reduce water loss and delay browning. The holding of the fruit in closed polyethylene bags versus a paper bag at 22°C significantly reduces water loss and browning by creating another barrier to water loss and a higher RH around the fruit. Low RH storage conditions, hence conditions with higher vapour pressure gradients leds to greater water loss. Similarly, holding fruit at 2°C where the vapour pressure gradient would be less will delay the onset of pericarp browning (Paull & Chen, 1987). There is also a strong relationship between storage RH and time (Y. M. Jiang & Fu, 1999a). Storage in plastic, foil, or multilayer bags is frequently reported to maintain pericarp colour better than coating with various organic acid and inorganic salt treatments (Reichel et al., 2017).

Commercially litchi fruit packed in corrugated boxes with PE film liners have a better appearance and longer storage life than those without PE film liners (Figure 3a vs. b) (Ketsa & Leelawatana, 1992b). To ensure the retention of pericarp color, various steps are employed. In Thailand, the fruit are hydrocooled before being loaded into reefer containers. This precooling greatly improves fruit quality, though this cold-shocked fruit might be more susceptible to chilling (Tongdee, 1998). An alternative to hydrocooling is forced air cooling, where air speed and RH of the cooling can influence water loss. A linear relationship is found between air speed and moisture loss (Bryant, 2012). At the highest wind speed of



FIGURE 3 Litchi postharvest handling: (a) fruit held in a carton with a plastic liner for 7 days at ambient temperature, (b) fruit held for 7 days at ambient temperature without a plastic liner, and (c) litchi fruit treated just with an acid dip (HCl 4% for 10 min) or SO_2 fumigation (1.5% for 12 min) followed by acid dip and Control 1. All stored for 30 days at 0°C and 5 days at 15°C. Control 2—Fruit stored 30 days at 0°C. (d) Litchi fruit right after SO_2 fumigation.

1.55 ms^{-1}, the moisture loss is sevenfold greater than in still air. Holding fruit at higher HR runs the risk of saprophytic fungal growth (Figure 3c). Another commercial treatment approved in some markets is SO_2 fumigation that stabilizes the anthocyanin, making them less susceptible to oxidation (Jurd, 1964). Rani et al. (2018) observed that SO_2 fumigated fruit precooled at 4°C for 4 h had a 5.6% decay after 41 days at 0°C, while without precooling, there was a 12% decay after 9 days.

SO_2 fumigation and physical damage increase microcracking (Sivakumar & Korsten, 2004). Fruit fumigated with sulfur dioxide show an increase in weight loss with more pericarp microcracks (Sivakumar et al., 2005), but browning does not occur. Hydro-cooling could reduce water loss, but it may enhance the decay problem with rapid cooling especially of warm fruit potentially causing more cracking as seen in other fruits (Vigneault et al., 2000). This risk may also apply to litchi. Olesen et al. (2003) reported that the air-cooled fruit had superior color, fewer rots, and less rot coverage than the hydro-cooled fruit but had a poorer hydration state. Fruit that are treated with hydrocooling before SO_2 treatment also have slightly higher levels of spoilage (Mhlophea & Kruger, 2014). Fruit that received a hydro-cooling treatment after sulfur fumigation had more fungal infections than the control.

At lower storage RH, Y. M. Jiang and Fu (1999b) found that the pericarp had greater PPO activity and lower total anthocyanin content, with a higher pH of the pericarp and increased browning (D. Zhang et al., 1997). PAL activity in the pericarp also increases when stored at a lower RH and had greater water loss (Y. M. Jiang & Fu, 1999a). Coupled with these changes under lower storage conditions, higher peroxide content, PPO and POD activities, lower total phenolic compounds, and glutathione (GSH) content are also observed, suggesting a reduction in antioxidant capacities and an increase in the oxidation of phenolics by PPO and POD. Humidification maintains the integrity of the cell membrane and thus limits PPO activity and respiration rate (Xiao et al., 2019). This supports the earlier report by X. M. Huang et al. (2005) of a significant positive correlation ($R^2 = 0.563$, $p = 0.002$) between membrane leakage and water loss in the pericarp in Huaizhi. However, the desiccation rates of different cultivars are not consistent with their fruit deterioration rate. The structural calcium content is negatively related to the rate of fruit deterioration and membrane leakage (X. M. Huang et al., 2005). The results suggest that calcium may influence fruit senescence through its role in desiccation tolerance and the maintenance of membrane integrity.

Low relative humidity may promote the loss of anthocyanins. The anthocyanins in Kom litchi, cyanidin-3-rutinoside, cyanidin-3-glucoside, and malvidin-3-glucoside all decline when the fruit is stored at RH <100%. In 100% RH, the anthocyanin content was greater (Somboonkaew & Terry, 2010). Glutathione sulfotransferases (GST) may also play an important role in litchi pericarp browning. The maximum expression of LcGST occurs within 24 h stored at 70% RH concurrent with the maximum GST activity (J. P. Zhang et al., 2014). At high RH, maximum LcGST expression and GST activity occur after 48 h under high RH. Under low RH conditions, the fruit loses water that triggers LcGST expression that leads to an increase in GST activity in response to cellular oxidation and browning related to water loss.

Senescence. Senescence or deterioration as the nonclimacteric litchi ages after it reaches a ripe stage and following harvest. The process is dominated by desiccation and breakdown of the pericarp membrane. The rates of these processes are accelerated once the fruit is detached initially from the tree and then from the panicle. Pericarp membrane leakage begins within 2 days after harvest and when kept at 26–30°C, occurring first in the mesocarp and 3 days later in the sclerenchyma exocarp cells (X. M. Huang et al., 2005). At 5 days after harvest, no membrane breakdown is seen in epidermal cells that have very high calcium content. The leakage of the pericarp membrane of fruit left attached to the tree is very low.

Membrane leakage and browning)parallel each other. In Guiwei, in addition to an increase in pericarp leakage, the activity of ANT, PPO, and POD; the content of malondialdehyde (MDA) and H_2O_2; and the rate of superoxide production also increase (Z. Zhang et al., 2015). At the same time, the content of anthocyanins and cyanidin-3-rutinoside, and the activities of CAT and DPPH radical-scavenging activity and reducing power decreased. The activities of superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione reductase (GR) activities initially increased and then decreased. Similar increases in pericarp leakage rate, MDA content, and pH value are reported for Feizixiao (J. Wang, Wang, et al., 2010). Along with the decrease in pericarp water content, also most pigments, including anthocyanin, flavonoid, phenols, chlorophyll a, total chlorophyll, and PPO activity, continuously declined. A slightly different pattern for POD was found that increased then decreased (J. Wang, Wang, et al., 2010). Concomitant with browning, loss of pericarp moisture and an increase in brittleness at 5°C, the activities of PPO and POD decline (Reichel et al., 2010). As an indicator of membrane leakage and oxidation, the pH of the pericarp rose from 4.5 to 5.3 as the anthocyanin content declined, at 25°C and room temperature (Chu et al., 2004; Pang et al., 2001b). Anthocyanin extracts have been shown to decolorize, turn brown, and become unstable as the pH increases (Pang et al., 2001b; Underhill, Simons, et al., 1992).

When fruit are stored at 4°C and 95% RH for 25 days, cell membrane integrity is maintained with PPO activity inhibited early in storage (Xiao et al., 2019). The total phenolic and procyanidin contents decreased by 20.2% and 24.2% at 4°C in 7 days and 37.8% and 47.8% when held at RT for 3 days, respectively. Anthocyanins are reduced by 41.3% and 73%, respectively, at 4°C for 7 days and RT for 3 days. Other reported changes in the pericarp during storage included a

decrease in oxygen radical absorbance capacity and cellular antioxidant activity of 17.6% and 58.7% at 4˚C, and by 23.4% and 66.0% at RT, respectively (Deng et al., 2018). Low-temperature storage limits the increase in the rate of pericarp leakage, though the membrane leakage rate increased continuously during low-temperature storage. When the fruit are returned to 25˚C, the membrane leakage rate increases rapidly (H. Liu et al., 2011), along with an increase in the browning index and a decrease in pericarp thickness, water content, and CIE a^* value (Reichel et al., 2013).

These changes during storage are associated with changes in gene expression. There were 1272 differentially expressed genes between stored and not stored fruit (Zhou et al., 2020). The authors were able to divide the expression pattern into a "senescence onset" stage and a "browning" stage. During the senescence onset stage, genes associated with senescence and stress response are significantly upregulated, while the browning stage was dominated by the upregulation of genes related to cell wall degradation, oxidation, and disease response. qPCR analysis of 30 selected differentially expressed genes showed that the expression patterns of the pericarp Huaizhi and Guiwei are similar and consistent with the RNA sequence results.

Chilling injury. Litchi is a subtropical fruit that shows chilling injury symptoms after a long period of storage at low temperature. The symptoms described include pericarp browning that is similar to that shown by water loss, and increase in decay susceptibility, though it is possible that small losses in pericarp water content may be involved and worsen the impact of low-temperature storage. Litchi stored at 1˚C for 12 days then transferred to 20˚C for 1 day rapidly show pericarp browning (Kader, 1998).

Storage recommendations for litchi vary widely, depending in part on the criteria used to judge chilling injury. Kader (1998) indicates that the optimal storage temperature is 5˚C but ranges from 1.5 to 10˚C, depending on the cultivar and the intended storage duration. Most studies support the optimal of 4–5˚C using criteria based on maintenance of pericarp colour and low decay rather than 1, 2, 3, 8, and 10˚C (Archibald & Bower, 2008; X. Y. Huang, Kang, et al., 1990; C. C. Huang et al., 1991; Olesen et al., 2003; Pornchaloempong et al., 1998). Outside of this range, includes Schutte et al.'s (1990) recommendation of 3.5˚C for Madras and Mauritius litchi in South Africa and W. X. Chen et al.'s (2001) recommendation of 3–5˚C in China. Tongdee (1998) in her storage studies in Thailand reported signs of chilling injury at storage temperatures below 4–7˚C. As discussed above, the commercial use of hydrocooling before storage in Thailand improves fruit quality retention, although the pericarp might be more susceptible to chilling, though hydrocooling especially of warm fruit could lead to greater microcracking and potential decay that maybe unrelated to chilling.

Nuomici and Guiwei stored at 0˚C for 14–21 days show chilling injury symptoms and a rapid increase in the browning index, and membrane leakage rate, while fruit stored at 3˚C have much smaller changes (W. R. Hu et al., 2004a, 2004b, 2006b). The major changes in the fruit of chilling injury at 0˚C are the rapid decline in the content of anthocyanin, flavonoids, and total phenols (W. R. Hu et al., 2004a; W. R. Hu, Pang, et al., 2005); the increase in MDA content was much faster (W. R. Hu et al., 2004b; W. R. Hu, Liu, et al., 2005); the content of polyamines (putrescine [Put], spermidine [Spd], spermine [Spm]) increased (W. R. Hu et al., 2006a); SOD, CAT, APX, and POD decreased, while lipoxygenase (LOX) and ANT increased rapidly (W. R. Hu et al., 2004b; W. R. Hu, Liu, et al., 2005; W. R. Hu, Pang, et al., 2005). Treatment with ABA, 1-MCP, and Spd all retard the development of chilling injury symptoms, including reducing the browning and membrane leakage rate. ABA treatment can also slow the decline of anthocyanins and reduce the activities of LOX and ANT (W. R. Hu, Liu, et al., 2005; W. R. Hu, Pang, et al., 2005, W. R. Hu, Liu, et al., 2010). Treatment with 1-MCP delays the decline of anthocyanins, reduces ethylene production, increases the activities of SOD and CAT activities in the early stage of storage, inhibits the increase of POD and APX activities in the later stage, and reduces PPO, LOX, and ANT (W. R. Hu, Liu, et al., 2005; W. R. Hu, Pang, et al., 2005; W. R. Hu et al., 2006b). Spermidine treatment reduces LOX activity and increases the content of the 3 polyamines in the pericarp (W. R. Hu, Liu, et al., 2005; W. R. Hu et al., 2006b).

Physical injury and disease. Physical injury and disease both enhance the brown of the pericarp. Mild and severe mechanical injuries can be produced by dropping litchi fruit 80 and 110 cm high, respectively. Both levels of injury accelerated the browning of the pericarp and accelerated flavour (TA and TSS). This injury can be detected by the E-nose from day 1 to day 4 after the injury (S. Xu et al., 2020). X. Li et al. (2005) have reported 65–90% of litchi fruit are latently infected by anthracnose in the pericarp at harvest. The higher the rate of preharvest anthracnose infection, the more serious the postharvest decay and fruit browning. It would be expected that abrasion damage in the field with fruit rubbing against each other, during harvest and postharvest handling, and packing could lead to breaking of the pericarp cuticle, increased rate of water loss and hence browning, and the opportunity for saprophytic growth when stored at high humidity or in fully sealed plastic bags. Fruit fly stings could also contribute to this loss.

Causes of pericarp browning

Litchi pericarp browning is generally regarded as being due to the oxidation of anthocyanins and phenolics into brown substances. This oxidative reaction is mainly enzymatic, especially the oxidation of phenolics by PPO and POD which was

a major focus in the 1980s and 1990s (Y. Jiang, 2000; Y. Jiang, Duan, et al., 2004; Z. F. Lin, Li, Lin, et al., 1988; Z. F. Lin, Li, Zhang, et al., 1988; Tan & Li, 1984; Underhill, 1992; J. B. Wang, Wang, & Jin, 2010; Zauberman et al., 1991). Subsequently, an ANT was purified and described as a key enzyme oxidizing anthocyanin leading to a change in perspective and emphasis of the enzymatic oxidation reactions (Z. Zhang et al., 2001, 2002; Z. Q. Zhang et al., 2003). Changes in membrane leakage and integrity leading to loss of cellular compartmentation of substrates and oxidative enzymes are essential for these reactions to take place (Y. Jiang, Duan, et al., 2004). Therefore, all factors that influence the stability of the membrane, such as the antioxidant capacity and energy status of the membrane, affect browning. This network of interacting factors influences and correlates with each other. In addition, non-enzymatic factors may be involved, though not reported.

Enzymatic oxidation.

Polyphenol oxidase (PPO). PPO can oxidize some polyphenols in the litchi pericarp. Partially purified litchi PPO can use polyphenols such as pyrogallol or catechol as substrates but not monophenols (Tan & Li, 1984). Tan and Zhou (1987) separately extracted litchi PPO and its natural substrate from the pericarp. When both extracts are combined, a brown pigment is obtained. The relative contents of flavonoids, phenolics, and anthocyanin in pericarp decreased by 41%, 29%, and 10%, respectively, during the 7 days that the pericarp browning occurred. PPO activity increases in the first 2 days and then declines, suggesting that PPO oxidized phenolics to produce brown pigments (Z. F. Lin, Li, Lin, et al., 1988). When purified litchi PPO is added to the phenolic extract, the phenol content in the extract decreased, while the absorbance at 410 nm increased, indicating phenol oxidation of phenol by PPO to form the brown pigment (Y. Jiang, 2000). The UV, 1H NMR, 13C NMR, and ESI-MS data identified (-)-epicatechin as a direct substrate for the PPO from litchi pericarp (Sun et al., 2006). The pericarp (-)-epicatechin content declines as the pericarp browning index increases (J. Sun, Jiang, et al., 2010). Pyrogallol, catechol, 4-methylcatechol (Y. M. Jiang et al., 1997), (-)-epicatechin, and procyanidin A2 (L. Liu et al., 2010; J. Sun, Jiang, et al., 2010) are also good substrates for PPO. It is concluded that enzymatic browning of the litchi pericarp occurs and involves PPO and polyphenols.

The PPO enzyme is composed of two similar subunits (Y. Jiang et al., 1999). The optimal pH for PPO activity is 6.8 with 4-methylcatechol as a substrate, with no activity observed at pH below 4. PPO has maximum activity at 65°C. Reduced GSH, L-cysteine, tropolone, thiourea, $FeSO_4$, $SnCl_2$, and citric acid markedly inhibited PPO activity, while MnSO4 and CaCl2 enhanced PPO activity (Y. M. Jiang, 2001; Y. M. Jiang et al., 1997; Y. Jiang et al., 1999). Histidyl, tryptophyl, and thiol groups, but not tyrosyl and lysyl residues, are essential for the catalytic activity (Y. M. Jiang, 2001).

The litchi PPO gene (LcPPO, JF926153) is expressed in the pericarp of newly harvested litchi fruit (J. Wang et al., 2014) more than in developing fruit. The level of LcPPO expression and the PPO activity in the pericarp of the postharvest fruit show similar variation. When the fruit is stored at room temperature without packaging, the pericarp browning index, PPO activity, and LcPPO expression in the pericarp were higher in Nandaowuhe, the most rapid browning, and the lowest in Ziniangxi, the slowest browning within 2 days after harvest. If the fruit are held in a plastic bag, browning is delayed as is pericarp PPO activity and LcPPO gene expression. Storage at 4°C, which also delays browning, similarly had reduced PPO activity and LcPPO gene expression. The results support a strong relationship between PPO gene expression, PPO activity, and pericarp browning.

Litchi PPO cannot directly oxidize anthocyanins, but in the presence of phenolics, it stimulates degradation leading to the development of brown pigments. Mixing PPO and anthocyanin extract gives no obvious changes with the addition of a phenolic extract, and anthocyanins are rapidly degraded (Y. Jiang, 2000). Similar findings have been reported by Pang et al. (2008) and Ruenroengklin, Sun, et al. (2009). This degradation of anthocyanin by PPO occurs in the presence of (-)-epicatechin, an endogenous PPO substrate, and catechol, an exogenous PPO substrate (J. Sun, Jiang, et al., 2010). The results of Pang et al. (2008) supported the conclusion that PPO did not directly oxidize anthocyanins but that some oxidized products, probable quinones generated by PPO's activity, catalyze the degradation of litchi anthocyanins nonenzymatically. Another reaction that could be involved in the degradation and browning is oxidation due to H_2O_2 and hydroxyl radicals, whose contents decline and then increase markedly as browning increased (Ruenroengklin, Yang, et al., 2009). Purified litchi anthocyanin is rapidly degraded by H_2O_2 and hydroxyl radicals. Combined with previous studies, the degradation of anthocyanins by PPO is accelerated in the presence of (-)-epicatechin and other phenolic substrates (Ruenroengklin, Sun, et al., 2009) and produces ROS (H_2O_2 and hydroxyl radicals) that degrade (oxidize) anthocyanins.

Another potential degradation pathway is through ANT. ANT enzymatically hydrolyzes anthocyanin to anthocyanidin and sugar, and the anthocyanidin is spontaneous transforming the aglucone pigment into colorless forms. These colourless forms are like catechol that can be oxidized by PPO (Z. Zhang et al., 2001). PPO oxidizes procyanidins also through a coupled oxidation pathway. L. Liu et al. (2010) reported that the procyanidins of litchi pericarp oxidize very slowly when incubated alone with PPO. However, (-)-epicatechin could accelerate the oxidation of procyanidins and the other flavanols through a coupled oxidation pathway. The published

data as to the overall significance of ANT in the breakdown and browning is unclear.

Fumigation with SO_2 completely inhibits litchi browning and prevents the loss of pigments; it also inhibits PPO activity (Zauberman et al., 1991). SO_2 combines with anthocyanin to form a stable anthocyanin-SO_3H complex (Jurd, 1964). Acid dip treatment also used in conjunction with SO_2 fumigation also inhibits peel browning (Zauberman et al., 1990, 1991) by reducing or inhibiting PPO activity (Y. M. Jiang, 2001; Y. Jiang, Li, et al., 2004; Lichter et al., 2000; Saengnil et al., 2006). Acid dip treatment also lowered the pH that can help stabilize anthocyanins (Pang et al., 2001a). Y. Jiang and Fu (1998), Underhill (1992), and Underhill and Critchley (1994) reported that treatment of litchi fruit with 10 mmol L^{-1} GSH combined with 100 mmol L^{-1} citric acid controls browning with a 80%–85% inhibition of PPO activity being observed. Ducamp-Collin et al. (2008) reported further that a 60% citric acid and chitosan dip also inhibits pericarp browning. The results here may differ from those mentioned above probably because of the higher concentration of citric acid used in these studies.

Peroxidase. There are relatively few reports on the role of POD in litchi pericarp browning. The POD activity in the pericarp of stored fruit increases consistently with the pericarp browning index and negatively with the anthocyanin concentration (Z. F. Lin, Li, Zhang, et al., 1988; Z. Zhang, Pang, et al., 2005). POD purified from litchi pericarp has a Ph optimum of 6.8 with catechol, 4-methylcatechol, and hydroquinone being good substrates (Gong & Tian, 2002). The PPO and POD in litchi pericarp had free and bound forms. Certain new isozyme bands of PPO and POD appeared along with litchi pericarp browning (Z. Wu et al., 1998). The activity of POD and PPO of the pericarp Bengal litchi is maximal at Ph 6.5 and 7.0, respectively, and no activity is detected at Ph 2.5 and 9.5. The preincubation of the enzyme extract for 45 min at Ph 2.5 or 9.5 completely inactivated the enzymes (Mizobutsi, Finger, Ribeiro, Puschmann, Neves, et al., 2010). Ribeiro et al. (2010) obtained the same result in the Brewster litchi.

POD likely plays an important role in pericarp browning (Gong & Tian, 2002). The in situ tissue-blot localization of the oxidative activity confirmed that the activity of PPO was in the epicarp, POD is mainly restricted to mesocarp vascular tissue of the mesocarp with some activity in the epicarp. Underhill and Critchley (1995) postulated that both PPO and POD activities are associated with litchi pericarp browning. This is supported by Y. M. Jiang and Fu (1999a) finding that under lower storage RH, the reduced content of GSH decreased, while peroxides increased, as is the activity of PPO and POD. These results imply that pericarp water loss-induced browning may be associated with reduced antioxidant capacities and an increase in the oxidation of phenolics catalyzed by PPO and POD.

PODs, like PPOs, can catalyze anthocyanin hydrolysis in a coupled oxidation reaction. The anthocyanin content decreases rapidly after the addition of guaiacol. Furthermore, anthocyanidin, produced by hydrolysis of the purified anthocyanin, could act as a substrate of POD. Therefore, the enzyme browning of the litchi fruit pericarp caused by POD can involve an anthocyanase–anthocyanin–phenolic–H_2O_2 reaction—H_2O_2 (Z. Zhang, Pang, et al., 2005). The nature of this complex may vary between POD and PPO as found in grape and pea that although both have high affinities to (-)-epicatechin and catechin, different sized binding motifs and key amino acids were involved in binding (Nokthai et al., 2010).

During storage for 29 days at 4°C, when browning started, POD activity increased in the exocarp and declined in the endocarp, but PPO activity occurred in both tissues and showed little changes (S. Huang, Hart, et al., 1990). PPO activity and POD activity remained high after storage and then declined (Reichel et al., 2013). After 52 days of storage, only 15% PPO activity remained, and 43% of the POD remained. Z. Zhang et al. (2015) found that in fruit kept at 25°C, the activities of POD and PPO both increased.

In addition to storage, the impact of other postharvest treatments on POD and PPO has been studied. A hot water treatment, followed by an oxalic acid dip, gave good browning inhibition; the activities of PPO and POD were reduced; and the total anthocyanins maintained (Saengnil et al., 2006). Hot water dips also enhanced the effectiveness of oxalic acid dips, which reduced PPO and POD activities. Ducamp-Collin et al. (2008) reported that after dip in 60% citric combined with chitosan solution and cold storage, the activities of PPO and POD increased slightly with a slight decrease in the content of anthocyanin. However, in Huaizhi, the activities of PPO and POD increased significantly with a significant decline in the anthocyanin content.

Anthocyanase and laccase. Z. Zhang et al. (2001) first identified an ANT in the pericarp of litchi fruit. This enzyme hydrolyzes the sugar of anthocyanin to produce anthocyanidin. Anthrocyanins are unstable and potential targets for oxidation. High ANT activity is found in the pericarp and thus might contribute to the browning of the pericarp. ANT activity is maintained at a high level and increases during pericarp browning (Z. Q. Zhang et al., 2003). Under the same conditions, PPO and POD activities increased gradually, implying that ANT is involved in anthocyanin degradation and pericarp browning. Z. Zhang et al. (2015) reported that a treatment with apple polyphenols suppressed the activities of ANT, POD, and PPO in treated fruit that had higher levels of anthocyanins and cyanidin-3-rutinoside and a lower membrane leakage rate. Higher ANT and PPO activities are found in Nuomici, which is sensitive to pericarp browning, compared to lower activity in the less susceptible Guiwei and Lanzhu

(Z. Q. Zhang et al., 2003). Similarly, Jingganghongnuo has slower changes in browning indices compared to Guiwei and Nuomici. Jingganghongnuo has a higher content of phenols and anthocyanins; lower ANT, LAC, PPO, POD, and PAL activities; and the expression of LcANT, LcLAC, LcPPO, LcPOD, and LcPAL (Tang et al., 2020).

The fruit stored at 0˚C developed a chilling injury, and the pericarp ANT activity increased and remained higher than in the control stored at 3˚C (W. R. Hu, Pang, et al., 2005). Meanwhile, the anthocyanin content decreased. Heat treatment that can induce pericarp browning also immediately increase pericarp ANT activity and decreases the anthocyanin content. Acid dips alone inhibit ANT activity and assist in retaining pericarp colour. The addition of an acid dip to a heat treatment retained the colour of the pericarp and inhibited anthocyanin degradation (Fang et al., 2013). Anthocyanin degradation enzyme (ADE), POD, and PPO activities in the pericarp are also dramatically reduced. A marked reduction in LcPOD gene expression also occurs. Heat treatment with hot water alone leads to rapid browning and about 90% loss of anthocyanin content. The activities of ADE, POD, and PPO in the pericarp remained similar to those of controls not heated or nonacid treated.

Another possible pericarp degradation pathway would be anthocyanin degradation enzymes (ADE) that is not PPO or POD (Cai et al., 2010). Purified ADE showed high activity for litchi anthocyanins, mainly cyanidin-rutinoside. The purified ADE was identified as laccase (ADE/LAC) (Fang et al., 2015). The level of expression of the ADE/LAC pericarp gene is 1000-fold greater than PPO. Anthocyanin degradation requires the presence of (-)-epicatechin and suggests an ADE/LAC epicatechin-coupled oxidation model. This pathway is supported by a dramatic decline in pericarp (-)-epicatechin that parallels the degradation of anthocyanin. ADE/LAC is located mainly in the vacuole along with phenolic substrates. This vacuolar localization and its high expression in the pericarp with epicatechin changes play an essential role in anthocyanin breakdown during pericarp browning.

Membrane factor. Membranes plays an important role in pericarp browning. The enzyme activity described above requires the disruption of cellular compartments that allows PPO located in chloroplasts and other plastids to react with phenolic substrates stored in the vacuoles to form brown polymers. Several external factors, such as water loss, chilling injury, and internal factors, such as oxidation states, and energy status, may act as triggers that alter membrane fluidity and permeability. Changes in these permeabilities result in the loss of subcellular compartmentation, leading to enzyme and substrate reactions to occur that lead to pericarp browning (Y. Jiang, Duan, et al., 2004).

The most common measure of membrane integrity is cell leakage. The membrane leakage of litchi pericarp after 20-day storage at 3–5˚C is doubled that following 10-day storage before browning occurs, indicating that the membrane leakage increases earlier than the browning of the pericarp (H. Liu et al., 2011). Similarly, Duan et al. (2011) observed that the membrane leakage rate increased, while the pericarp did not turn brown for litchi fruit kept at 28˚C, 90%–95% RH for 2 days. The browning index and membrane permeability increased as storage time increased in the three evaluated cultivars, and membrane permeability is positively related to the browning index (X. Xu et al., 2005).

Membrane oxidation and cellular energy status influence leakage. The litchi fruit transferred from 3–5˚C to 25˚C had an increase in lipase, phospholipase D (PLD), and LOX, and ATP, ADP, and adenylate energy charge (AEC) also increased (H. Liu et al., 2011). Following longer storage time, the ATP and AEC content is lower in the pericarp, and the higher the activity of the lipid oxidative enzymes, and a higher membrane permeability. Increasing storage time at 3–5˚C increases the activity of oxidative enzymes while resulting in an energy shortage that reduces membrane integrity, resulting in accelerated browning (H. Liu et al., 2011).

Antioxidant state. Anthocyanin, flavonoid, total phenols, and antioxidant capacity, such as superoxide radicals, hydroxyl radical and DPPH free radical scavenging activity, and reducing ability, all contribute to the antioxidant status. The antioxidant enzyme activity includes SOD, APX, and CAT. A higher antioxidant status improves the maintenance of membrane stability. High levels of oxidants promote membrane deterioration. The oxidant level is determined by the ROS levels (H_2O_2, superoxide anions, hydroxyl radical); the activity of oxidative enzymes such as lipase, LOX, and phosphatase PLD; and the saturated fatty acid content and the MDA content.

The antioxidant status of the pericarp gradually declines after harvest (Duan et al., 2011). This decline is associated with reduced power levels and free-radical scavenging ability against DPPH, superoxide anions, and hydroxyl radicals. This occurs with a decrease in anthocyanins and phenolic compounds with storage. There is a linear relationship between anthocyanins or phenolic compounds and the antioxidant ability or free radical scavenging activity (Duan et al., 2011). After 10–20 days of storage at 3–5˚C, the pericarp does not show browning, although the membrane leakage is higher at 20 days than at 10 days. At 30 days, the permeability was even higher, suggesting a gradual change in membrane stability. Immediately the fruit returned to 25˚C; the pericarp rapidly turned brown; and membrane permeability and lipase, PLD, and LOX activities also increased markedly. The longer the fruit are stored, the more rapid changes there were when returned to 25˚C, indicating that these oxidant enzyme activities are continuously activated at low temperatures (H. Liu et al., 2011).

The pericarp of Ziniangxi turns brown slower than other cultivars and has lower MDA content, membrane leakage

rate, LOX and CAT activities, and a higher GR activity in the pericarp (Xiao et al., 2011). Feizixiao has the most severe browning and disease incidence with the highest relative membrane leakage, along with the highest increase in PLD activity and acid phosphatase activity. When Feizixiao is stored for 6 days, the (-)-epicatechin and procyanidin A2 content and the activities of POD, APX, and SOD are lower than in Heiye and Xiangli (J. Sun et al., 2012).

The pericarp browning index increases as the storage time is extended at 25˚C and there is an increase in relative membrane leakage, the activities of ANT, PPO, and POD, the contents of H_2O_2, MDA and the superoxide production rate, while the contents of anthocyanin, cyanidin-3-rutinoside decrease (Z. Zhang et al., 2015). The activities of SOD, APX, and GR increased and then decreased. CAT, DPPH radical scavenging, and reducing power activities all declined (Z. Zhang et al., 2015). J. Wang, Wang, et al. (2010) had reported similar findings and found that the PH value increased. The content of anthocyanin, flavonoid, phenols, chlorophyll a, and total chlorophyll decreased with the PPO activity continuously declining, while the activities of CAT and SOD showed a variable pattern first and then declining before increasing again.

Water loss accelerates pericarp browning (Campbell, 1959; Underhill & Critchley, 1993b, 1994), with a good correlation between membrane leakage and pericarp water loss (X. M. Huang et al., 2005). Water loss increases membrane leakage and reduces the antioxidant capacity, including lower anthocyanin, GSH content, and higher ROS content (Y. M. Jiang & Fu, 1999a; Somboonkaew & Terry, 2010; Xiao et al., 2019; J. P. Zhang et al., 2014). However, X. M. Huang et al. (2005) reported varietal differences with desiccation rates not consistently following the fruit deterioration rate. The authors felt that the difference in the calcium content was negatively correlated with the rate of fruit deterioration rate and membrane leakage. Calcium might delay fruit senescence, increase tolerance to desiccation, and maintain membrane integrity.

Chilling injury similarly promotes membrane leakage. Nuomici develops chilling injury symptoms after storage at 0˚C for 21 days, and the browning index and membrane leakage are higher than fruit stored at 3˚C (W. R. Hu et al., 2004a). After 14 days at 0˚C before symptoms of chilling injury occurred, the SOD, POD, APX, and CAT activities decreased and MDA increased, while the activities of the same enzymes at 3˚C remained high (W. R. Hu et al., 2004b). The increase in LOX activity and MDA content is higher in fruit stored at 0˚C than at 3˚C.

AsA has a protective effect on both anthocyanin and phenols in the pericarp. The browning index increases along with the decline in AsA content (Y. Jiang, 2000). When anthocyanin and phenolic extracts are mixed with PPO, the anthocyanin content remains unchanged as long as there is AsA present. Once AsA is consumed, the destruction of anthocyanin begins and the oxidized products of the phenolic extracts also begin to be produced. A coating with an aloe vera gel reduced the browning index, weight loss, superoxide anion, relative electrolyte leakage, H_2O_2, MDA content, POD, and PPO activities (Ali, Khan, Nawaz, et al., 2019). The coated fruit also had a higher total anthocyanin and AsA content; a total phenolic concentration; and higher activities of CAT, SOD, and APX along with higher TSS and TA.

Treatment with a variety of chemicals has shown broad effects on antioxidant status. Treatment with ABA, Spd, or 1-MCP retards LOX activity in the pericarp of fruit stored at 0˚C and tends to alleviate chilling injury. Dipping fruit in hot water increases the browning index and LOX activity (W. R. Hu, Liu, et al., 2005). However, a 4% HCl drop retards the browning of the pericarp, along with the limiting LOX activity. These results indicated that LOX plays a role in causing membrane damage and browning of litchi pericarp (W. R. Hu, Liu, et al., 2005). Melatonin treatment suppresses pericarp browning and reduces the relative rate of membrane leakage (Y. Zhang, Huber, et al., 2018). The melatonin effect was attributed to the improvement in antioxidant capacity and modulation of the repair of oxidatively damaged proteins. Melatonin inhibits the generation of superoxide radicals, H_2O_2, and MDA, thus delaying the loss of total phenolics, flavonoids, and anthocyanins and increasing the activities of antioxidant enzymes (SOD, CAT, APX, and GR) and reducing the activities of PPO and POD. Four genes encoding enzymes for repair of oxidized proteins, including LcMsrA1, LcMsrA2, LcMsrB1, and LcMsB2, are upregulated.

Hydrogen water treatment, prepared by a hydrogen-rich water generator, delays pericarp browning, a possible consequence of the induction of antioxidant system-related characters, and directly or indirectly enhance the antioxidant capacity at 25˚C (Yun et al., 2021). Twenty-five characters related to the antioxidant system were identified. The pericarp of the treated fruit had higher levels of superoxide radical scavenging activity, GSH, monodehydroascorbate reductase (MDHAR), PPO, and total flavonoids during storage, with higher levels of H_2O_2, CAT, glutathione disulfide (GSSG), ascorbate oxidase, and total phenols only on day 1, and higher APX, GR, glutathione peroxidase (GPX), and higher levels of total anthocyanin at the later stage of storage.

An acidified calcium sulfate (ACS) dip effectively prevented pericarp browning (C. Y. Wang, Chen, et al., 2010). The activities of PPO and POD are inhibited, and there is an increase in total phenolic and total anthocyanin contents. The radical scavenging activities of ROO•, DPPH•, hydroxyl radical, and superoxide anions are also enhanced following ACS treatment. Higher activities of several antioxidant enzymes and enzymes of the ascorbate-glutathione cycle, including CAT, APX, GPX, dehydroascorbate reductase (DHAR), and MDHAR, are maintained during storage. The content

of flavonoids and the three major flavonoids, cyanidin-3-rutinoside, cyanidin-3-glucoside, and quercetin-3-rutinoside, are also higher after treatment.

Treatment of pyrogallol, a catechin with high superoxide anions scavenging activity (Furuno et al., 2002), reduces browning and delays fruit rot. The respiratory rate and the activities of POD and PPO are reduced, and there is a delay in the loss of membrane permeability during the activity of PAL. There is a delay in the loss of anthocyanin and phenolics, and higher DPPH radical scavenging activity, reducing the power and concentration of the four phenolic compounds procyanidin B1, (+)-catechin, (-)-epicatechin, and (-)-epicatechin-3-gallate, is maintained (Jing et al., 2013). Treatment with n-butanol, a specific inhibitor of PLD, retards browning and disease index and decreases PLD, PAL, and POD activities and MDA content while enhancing APX activity (J. Sun et al., 2011).

Pure oxygen treatment retards pericarp browning and increases membrane permeability (Duan et al., 2011). The lipid peroxide content is reduced, and there is a delay in the increases of the H_2O_2 content and superoxide production rate while enhancing the activities of SOD, APX, and CAT. Treatment increased the antioxidant ability possibly related to higher levels of anthocyanins and phenolic compounds. The authors suggest that enhanced antioxidant activity and antioxidant enzyme induced by pure oxygen may contribute to alleviating lipid peroxidation and maintaining membrane integrity (Duan et al., 2011). The application of 6-benzylaminopurine (BAP) inhibited decay incidence by *Peronophythora litchii*, the main pathogenic fungi. The lower browning of the pericarp in treated fruit is associated with reduced PPO activity, increased PAL activity, and higher levels of anthocyanin and total phenolic compounds. Treatment with BAP reduces H_2O_2 accumulation and lipid peroxidation and improves the activity of SOD, CAT, APX, and DPPH, leading to less ROS accumulation and lipid peroxidation (D. Zhang, Xu, et al., 2018).

Treatment with apple polyphenols reduces pericarp browning; suppresses ANT, PPO, and POD activities; and increases anthocyanins and cyanidin-3-rutinoside content. The treated fruit have a lower membrane leakage rate due to reduced oxidative damage and reduced MDA content and ROS generation. The activities of antioxidant enzymes (SOD, CAT, APX, and GR) and the nonenzymatic antioxidant capacity (DPPH radical scavenging activity and reducing power) are enhanced (Z. Zhang et al., 2015). Apple polyphenols have been shown to delay the development of litchi pericarp browning, reduce the respiration rate and weight loss, and slow the changes in glucose and fructose contents while inhibiting the decline in sucrose. The treated fruit has a higher content of organic acids, phenolic, AsA, and GSH (Z. Su et al., 2019). The improved antioxidant capacity of these treated fruit is indicated by the increased radical scavenging activity of DPPH and FRAP.

Treatment with nitric oxide (released from sodium nitroprusside) reduces pericarp browning, weight loss, and MDA content, with a higher anthocyanin content and levels of total phenolics and antioxidant capacity (Barman et al., 2014). Treatment also delayed the loss of TSS, TA, and AsA in fruit with a minimum level of decay. Nitric oxide treatment also retarded the activities of both PPO and POD (Kramchote et al., 2008).

A preharvest application of 5-aminolevulinic acid (5-ALA), a precursor in the biosynthesis of porphyrin compounds, and a plant growth regulator significantly increased postharvest fruit anthocyanins, total phenol, vitamin C, and antioxidant activity (Feng et al., 2015). Treatment with sodium para-aminosalicylate (PAS-Na) inhibited pericarp browning and potentially reduced the respiration rate by inhibiting ROS-mediated senescence (T. Li, Shi, et al., 2019). Additionally, PAS-Na treatment improved the activities of SOD, CAT, and GPX. Fruit pericarp also have a reduced membrane leakage rate and MDA content and lower LOX activities. Thidiazuron (TDZ) inhibits anthocyanin accumulation but does not significantly alter antioxidant activity (Zeng et al., 2012). All treatments significantly reduce the browning index, leakage rate, and PPO activity after storage. A membership function analysis (fuzzy subsets) indicates that the preharvest 5-ALA application is the most beneficial for maintaining quality postharvest.

There are still many other reports indicating that various chemical treatments are beneficial for increasing antioxidant capacity; are conducive to maintaining membrane integrity; and can effectively reduce pericarp browning, including L-cysteine (Ali, Khan, & Malik, 2016), kojic acid (Shah et al., 2017), methionine (Ali et al., 2018), chitosan (D. Zhang & Quantick, 1997), polyamines (Y. M. Jiang & Chen, 1995), and ABA (W. R. Hu, Liu, et al., 2010).

Energy state. Maintaining membrane stability is an associated state of cell energy. This energy state is determined by the content of ATP and adenylate energy charge (AEC) (ATP, ADP, and adenosine monophosphate [AMP] concentrations) for homeostasis between 0.7 and 0.95 coupled to high H^+-ATPase, Ca^{2+}-ATPase, succinate dehydrogenase (SDH), and cytochrome C oxidase (CCO) activities. Low energy levels (AECs) adversely affect membrane stability.

As pericarp browning occurs with an increase in membrane permeability during cold storage, the content of ATP, ADP, and AMP and the AEC value decline. This imbalance in energy status accelerates fruit deterioration and early senescence (H. Liu et al., 2011). Energy deficiency leads to a burst in fruit respiration to achieve homeostasis. The respiratory burst is associated with an increase in reactive oxygen species, POD activity, and the initiation of the LOX pathway (Yun et al., 2016). Pure oxygen exposure delays the increase in membrane permeability and inhibits pericarp browning.

Application of DNP, prior to exposure to pure oxygen, accelerates membrane integrity loss and the appearance of pericarp browning. Pure oxygen treatment increases respiration and CCO activity while maintaining high ATP levels (Shi et al., 2008). The importance of ATP to membrane integrity is shown by exogenous ATP treatment, which reduces the increase in membrane leakage by delaying pericarp browning, with the proton pumping inhibitor DNP having the opposite effect on leakage and browning. ATP treatment also negatively regulates the expression of alternative oxidase 1 (AOX1) that increased after 2 days of storage. There was no effect of ATP treatment on the expression of ADP/ATP carrier 1 (AAC1) that imports ADP into mitochondria and slows the changes in gene expression of sucrose non-fermenting-1-related kinase 2 (SnRK2) involved in abiotic stress responses (H. Wang et al., 2013). Jingganghongnuo has a slow pericarp browning compared to Guiwei and Nuomici with the highest AEC and expression of the metabolic ATP-related genes LcATPb, LcSnRK2, LcAAC1, and LcAOX1 (Tang et al., 2020).

Litchi fruit show early browning, higher disease incidence, MDA content, and membrane leakage rate when inoculated with *P. litchii*. ATP treatment delays these changes and increases ATP content and energy charge levels, while DNP treatment accelerates the process of senescence and disease development (Yi, Qu, Jiang, Duan, et al., 2008; Yi, Qu, Jiang, Shi, et al., 2008). Enzymes involved in membrane lipid peroxidation and hydrolysis, such as PLD, acid phosphatase, and LOX, are lower in ATP-treated fruit. ATP-treated fruit before inoculation with *P. litchi* have higher antioxidant enzyme activities, including CAT, SOD, and APX, with higher DPPH scavenging activities, reducing power and phenolic content, while DNP treatment lowers the enzymes activities, scavenging ability, and phenolic compounds. In conclusion, it was suggested that ATP levels regulate the antioxidant system and that sufficient available energy is central to inhibiting browning and maintaining resistance to disease (Yi et al., 2010).

In addition to ATP and DNP that influence the energy charge, several other treatments have been applied to maintain the energy charge and membrane integrity. Z. Zhang et al. (2017) showed that tea seed oil treatment delays pericarp browning and maintains membrane integrity. This response was attributed to an effect on energy status as treatment increased the pericarp ATP level, energy charge, and activities of H^+-ATPase and Ca^{2+}-ATPase. In addition, the expression of LcAtpB, LcAAC1, LcAOX1, and LcSnRK2 is increased. Treatment with DNP increased CCO, H^+-ATPase, and Ca^{2+}-ATPase, leading to lower energy charges and early fruit senescence. On the contrary, ATP treatment reduced CCO activity, maintained a higher energy charge, and delayed browning (Z. Y. Gao, Zhao, et al., 2018). Z. Gao, Hu, et al. (2018) found that genes including LcSnRK2 and LcAAC1 are sensitive to changes in energy charge and could respond rapidly to an energy charge deficit and induced upregulation in expression. The upregulation of the LcAOX1 and LcUCP1 genes is positively correlated with fruit senescence.

Melatonin treatment retards pericarp browning and reduces membrane leakage changes potentially attributed to membrane lipid and energy metabolism (G. Liu et al., 2020; T. Wang et al., 2020). Melatonin treatment suppressed the increase of PLD, lipase, and LOX activities, preventing the hydrolysis of phosphatidylcholine into phosphatidic acid, increasing the content of unsaturated fatty acids (oleic acid, linoleic acid, and linolenic acid), lowering saturated fatty acids (palmitic acid, stearic acid) content, and maintaining higher energy status (T. Wang et al., 2020). The latter energy status is indicated by the higher ATP content and energy charge due to enzymes related to energy metabolism, including H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO. Melatonin treatment also suppresses the increase in leakage rate and MDA content, slow the decline in cellular energy level, as evidenced by a higher ATP content and a higher energy charge (G. Liu et al., 2020). This is similarly associated with energy metabolism enzymes including H^+-ATPase, Ca^{2+}-ATPase, SDH, and CCO. There is an increase in proline accumulation due to increased activities of ornithine–aminotransferase (OAT) and D1-pyrroline-5-carboxylate synthase (P5CS) and suppressed activity of proline dehydrogenase (PDH) (G. Liu et al., 2020).

Treatment with choline chloride (ChCl) also significantly inhibits pericarp browning and delayed programmed cell death (T. Li et al., 2020). As a constituent of membrane phospholipids, ChCl with a reported role in stress tolerance, application of ChCl to litchi pericarp decreases DNA laddering, inhibits the expression of programmed cell death-related genes, and maintains higher soluble protein content. ChCl treatment maintains a higher ATP content and energy charge in the pericarp as a result of a higher level of glycine betaine. Genes associated with energy metabolism and ATPase activities result in lower accumulation of ROS by improving the activities of SOD, CAT, and APX (T. Li et al., 2020).

Reaction of SO_2 and acid. SO_2 fumigation (Fuchs et al., 1993; Lichter et al., 2000; Luo et al., 2019) and an acid dip (Y. Jiang, Li, et al., 2004; Zauberman et al., 1990) effectively inhibit browning. Their effect is directly on anthocyanin and the enzymes that cause browning, not on the membranes.

Non-enzymatic oxidation. There are few reports related to the nonenzymatic oxidation of litchi pericarp browning. Purified litchi anthocyanin is degraded in the presence of H_2O_2 or hydroxyl radicals (Ruenroengklin, Yang, et al., 2009). Increasing the concentration of H_2O_2 or hydroxyl radicals increases the degradation of anthocyanin, the hydroxyl

radical being more effective. H_2O_2 and hydroxyl radicals can be products of the oxidation of phenols by PPO. The authors proposed that the browning of the pericarp could be based on the indirect oxidative degradation of anthocyanin caused by a PPO reaction product. The degradation of anthocyanin by H_2O_2 or hydroxyl radicals is more rapid at higher PH (Pang et al., 2001a, 2001d). Reducing agents, such as AsA, dithiothreitol, and Cys, do not slow the oxidation phenomena; they can also promote degradation and discolouration (Pang et al., 2001d). Decreasing peel PH by acid treatment inhibits browning (Zauberman et al., 1990). However, during senescence, there is an increase in the overall PH of the pericarp that is dominated by vacuolar PH, where the anthocyanins are found. This change in PH could lead to the gradual conversion of anthocyanin into colourless carbinol base and result in browning (Underhill, Simons, et al., 1992).

Sulfur dioxide (SO_2).

Effect of SO_2. Sulfur dioxide fumigation effectively inhibits the browning of the litchi pericarp. The pericarp after SO_2 treatment remains pliable but is initially bleached to a pinkish cream (Figure 3d) and turns a uniform pink after 3–5 days at 22˚C (Holcroft et al., 2005; Zauberman et al., 1990). The final red colour is permanent (Swarts, 1983).

Reaction of SO_2. Sulfur dioxide initially bleaches anthocyanins by the anthocyanin carbonium ion (R+) reaction and forms a colourless chromen-2 (or 4)-sulfonic acid (R- SO_2H). This complex has a structure and properties similar to those of an anthocyanin carbinol base (R-OH). This reversible process does not involve hydrolysis of the 3-glycosidic group, reduction of the pigment, or addition of bisulfite to a ketonic derivative of chalcone (Jurd, 1964). Timberlake and Bridle (1967) further reported that a complex is formed between sulfur dioxide and the flavylium cation (F+). This complex is stable at pH 1.05 and is reduced by hydroxylation of the seven and five positions of the flavylium structure with an increase in hydroxylation of the three-position anthocyanin. The anthocyanins form the weakest complexes of those compounds generated. Sodium metabisulphite can replace SO_2 fumigation and similarly inhibit pericarp browning (Duvenage et al., 1995; Sivakumar et al., 2005). The response is likely due to the formation of the same anthocyanin-SO3 complex. Treatment with sodium bisulfite and sodium diethyldithiocarbamate inhibits litchi PPO activity (Tan & Li, 1984). PPO activity was completely inhibited by SO_2 fumigation in litchi fruit (Zauberman et al., 1991).

Pericarp colour recovery can be achieved by desulfurization (DS) after SO_2 fumigation (SF). The effect is similar to the ability of SO_2 treatment to control rots and pericarp browning. More importantly, this desulfurization treatment greatly reduced aril sulfite residue. Several enzymes are responsible for the detoxification of sulfite and include sulfite oxidase, sulfite reductase, serine acetyltransferase, and o-acetylserine (thiol) lyase. These enzymes and their encoding genes increase after SO_2 fumigation and then decline as the resides decline suggesting they play a key role in sulfite metabolism (Luo et al., 2019).

Low pH.

Effect of low pH. The acid dip lowers the pH of the pericarp resulting in complete inhibition of browning (Lichter et al., 2000; Underhill & Critchley, 1994; Zauberman et al., 1990). This acidification of whole fruit increased the redness of the pericarp (Figure 3c), whereas an alkaline treatment caused rapid discolouration. These colour changes are reversible and are independent of anthocyanin synthesis and degradation, but Zauberman et al. (1991) reported that acid treatment is not effective when the fruit turns brown, that is, after anthocyanin degradation. The results support the view that increasing the pH of the pericarp after harvest leads to a process of decolourization of the anthocyanin that is independent of tissue browning (Underhill & Critchley, 1994). The colourless anthocyanin products are then oxidized to brown pigments as discussed above.

Different degrees of pericarp browning are produced by storing litchi fruit at different temperatures and humidity. Parallel to tissue browning, the pericarp pH increases from 4.15 to 4.74, and a significant correlation is seen between the red hue and the pH of the pericarp homogenate (Underhill & Critchley, 1994). The increased pH likely reflects changes in the vacuole pH, as the mesocarp parenchyma is highly vacuolated. As PH increased, the anthocyanin decolourized, turned brown, and became unstable (Chu et al., 2004; Pang et al., 2001b; Z. Zhang et al., 2001). After holding fruit for 4 days at room temperature, the pH of the pericarp increased from 4.19 to 4.88, the anthocyanin content decreased rapidly, from 0.169 to 0.072 mg g^{-1} FW, and the brown index rose markedly, from 1.00 to 4.86 (Pang et al., 2001b). Other researchers have reported greater increases in the PH of the pericarp homogenate. Pericarp homogenate increased from 4.0 to 6.2, while ascorbic acid content declined during long-term storage (M. X. Wu et al., 2001). pH plays a critical role in structure and stability, which in turn affects the browning of the pericarp (Underhill, Simons, et al., 1992).

Acid treatments are effective in preventing pericarp browning only if the pH of the pericarp is lowered to about 3.0. Litchi fruit that are first dipped in hot water and then in three different acid solutions showed that 10% oxalic acid was the most effective in controlling browning (Saengnil et al., 2006). The pH of the 10% oxalic acid solution was 0.82–1.25, and the pericarp pH after treatment was reduced to 2.11 from 4.28. Hot water dips increased the effectiveness of oxalic acid dip. Without hot water dip before oxalic acid treatment, the pH

pericarp was still high (pH 3.22), and the anti-browning effect is much less. With other acids, including citric acid and AsA, the pH of the solution is higher than that of oxalic acid, and the pericarp pH was 3.2 to 4.1, and the antibrowning effect is poor. Terdbaramee et al. (2003) found that 1.0 M citric acid (~20% w/v) dip (20% w/v) prevents pericarp browning during storage at 5°C. The pH of the pericarp was about 2.7 after dipping lower than pH lowered below the 3.3 pH found by Saengnil et al. (2006) with a 15% citric acid solution. Ducamp-Collin et al. (2008) used a 60% citric and 0.75% chitosan dip that prevented pericarp browning. The pH of the pericarp after dipping was 3.42–3.73, which is higher than in other reports. Very low concentrations of oxalic acid (2 and 4 MM) have been shown to delay pericarp browning (X. Zheng & Tian, 2006), although it was possibly due to increased membrane integrity, inhibition of anthocyanin degradation, decline of oxidation, and maintenance of low POD activity in fruit during storage.

Reaction of low pH. Anthocyanins are located in the vacuole, and the PH of the vacuoles rises along with the senescence or dehydration of the litchi pericarp from about pH 4.3. The high PH condition converts the structure of anthocyanins into a colourless form (carbinol) and reduces their stability (Chu et al., 2004; Pang et al., 2001a; Underhill, 1992; Z. Zhang et al., 2001).

The colour of the anthocyanin extract depends on the pH of the solution. Litchi pericarp anthocyanins are red at PH 1.47, orange at pH 3.30, became decolourized at PH 4.69, and turned brown at PH 7.01 (Pang et al., 2001a). After 20 days at room temperature, the anthocyanin degradation at PH 1.47, 3.30, 4.69, and 7.01 was 24.5%, 60%, 79.5%, and 100%, respectively. These results highlight the instability of litchi anthocyanins that become colourless and then turn brown as the medium pH increases. If 2 MM H_2O_2 was added to these solutions, 97.6% of the anthocyanins degraded in 20 h at pH 5.0. About 72.3% of the anthocyanins degraded in 30 h with 20 μM superoxide anions. At pH 1.0, the percentage of degradation is lower. Z. Zhang et al. (2001) calculated the half degradation constants for anthocyanins at different pHs of 1, 3, and 5, and they were 29, 15.3, and 10.5 days, respectively, indicating greater stability at lower pH. The pH of the litchi pericarp increased to 5.3 during 5-day storage at 25°C from pH 4.3 in the air of fruit transported for 4 days from China to Canada.

Anthocyanins returned to their original redness and concentrations if placed in a pH 4 solution for 5 days. This did not occur if the pH of the solution ranged between 5 and 6 for 5 days (Chu et al., 2004). The effect of pH on the colour of the pericarp seems to be directly on the anthocyanins, and the effect of the membrane is not significant. The leakage of the membrane is much higher in fruit dipped in 2% HCl than that dipped with 1% HCl, but the effects on maintaining the red pericarp and preventing browning were the same (Y. Jiang, Li, et al., 2004).

Acid dip significantly inhibited PPO and POD activities and greatly help maintain fruit color (W. R. Hu et al., 2004c). Treatment with 1% HCl markedly inhibits PPO activity and maintained a high anthocyanin content in litchi fruit pericarp tissue (Y. Jiang, Li, et al., 2004). As mentioned above, the soak of oxalic acid after a hot water dip reduces the activities of PPO and POD, maintained a high level of total anthocyanins, and significantly inhibited browning. Hot water dip increases the effectiveness of oxalic acid dip (Saengnil et al., 2006). The activity of PPO and POD is maximal at pH 7.0 and 6.5–6.7, respectively (Y. M. Jiang et al., 1997; Mizobutsi, Finger, Ribeiro, Puschmann, Neves, et al., 2010; Ribeiro et al., 2010). No PPO or POD activity is detected at pH 2.5. If enzyme extracts are pre-incubated for 35 or 45 min at pH 2.5, complete enzyme inactivation occurs (Mizobutsi, Finger, Ribeiro, Puschmann, Neves, et al., 2010, Mizobutsi, Finger, Ribeiro, Puschmann, Vieira, et al., 2010; Ribeiro et al., 2010). Low pH treatments are beneficial for maintaining the phenol content. A coating based on organic acids (citric or tartaric) at PH 0.8, 1.0, and 1.3 indicated that the browning rate is related to the rate of dehydration during storage and the pH of the pericarp. The lower the pH, the higher the total contents of phenols and anthocyanin in the pericarp (Joas et al., 2005).

ANT activity is similarly inhibited by acid treatments. A 4% HCl drop inhibits ANT activity and maintains pericarp redness (W. R. Hu, Pang, et al., 2005). An acid dip in 2% HCl after a 70°C hot water treatment for 20 s substantially protected the colour during storage at 25°C. The PH values in the pericarp of the heat-acid-treated fruit dropped to 3.2. This treatment dramatically reduced the activities of the expression of the ADE (ANT), POD, PPO, and LcPOD gene expression (Fang et al., 2013). Ducamp-Collin et al. (2008) reported that after 60% citric acid–chitosan treatment followed by cold storage, the PPO, POD, and ANT activities and the content of cyanidin-3-rutinoside and cyanidin-3-glucoside in the litchi fruit did not change significantly. In Wai Chee (Huaizhi), PPO, POD, and ANT activities increased, while the content of cyanidin-3-rutinoside and cyanidin-3-glucoside decreased. These results are different from those of the reports mentioned above where PPO, POD, and ANT activities are delayed by acid treatments. The differences may be related to the citric acid solution used here, which had a high viscosity and contacted fruit for a longer time.

Acid dip after SO_2 fumigation.

Effect of an acid dip after SO_2 fumigation. SO_2 fumigation, followed by a dip in HCl, delivers fruit of superior quality to SO fumigation only (Duvenage et al., 1995; Zauberman et al., 1990). SO_2 fumigation alone inhibits browning, resulting in a pliable but bleached peel that turns uniform pink

after 3–5 days at 22°C (Zauberman et al., 1990). After acid dip following SO_2 fumigation, the bleached fruit recovered its colour right after the acid dip in low pH solutions (Zauberman et al., 1990). No deterioration in the colour of the pericarp is observed after 12 weeks of storage after SO_2 fumigation and acid dip (Underhill et al., 1994). The pH and the colour are affected by the pH of the acid solution and the treatment time. Fumigation inhibits PPO activity but did not affect POD activity. The treatment must be performed on fruit that still have a red pericarp, and it is not possible to recover the red pericarp from already brown fruit by acidification (Zauberman et al., 1991).

The reaction of an acid dip after SO_2 fumigation. SO_2 fumigation caused rapid bleaching of the pericarp due to the formation of a colourless anthocyanin–SO H complex (Jurd, 1964). Acidification of the pericarp with an HCI dip results in an immediate improvement in the pericarp colour of the sulfur dioxide-treated fruit. Acidification is suggested to reverse the bleaching effect by promoting sulfur dioxide disassociation from the pigment complex. Increased pigment stability is due to acid-induced structural changes, and possible Cl-ion inhibition of PPO activity may also contribute to colour improvement (Underhill et al., 1994).

Acid dip after SO_2 fumigation strongly inhibits PPO activity but has no significant effect on POD activity (Zauberman et al., 1991). Dipping with sodium metabisulfite, to replace SO_2 fumigation, followed by HCl dip, also effectively delays pericarp browning. PPO and POD activities are again greatly retarded (Liang et al., 2012). Furthermore, the acid drop after SO_2 fumigation further reduces the pH value. The pH of the pericarp after SO_2 fumigation was about 5.8 versus 6.1 in untreated fruit, about 5.0 in acid-dipped fruit, and approximately 4.1 in acid-dipped after SO_2 fumigation fruit (Zauberman et al., 1991). A similar result is obtained; the pH of untreated fruit is 4.6, while it was 3.9 after SO_2 fumigation and 2.8 after an acid dip after SO_2 fumigation (Underhill, Bagshaw, et al., 1992).

Fruit treated only with an acid dip develops a red background but with brown patches on the pericarp. A uniform red pericarp is achieved when fruit are with an acid dip after SO_2 fumigation. SO_2 fumigation does cause damage as there is 80% leakage of electrolytes from the pericarp, while only 25% leakage occurs in nonfumigated fruit pericarp. This significant increase in membrane permeability presumably enables the penetration of the acid through to the cell vacuoles, where the anthocyanins are located, and/or pigment leakage from the vacuole to the acidified cell walls of the fruit pericarp. Fresh, nonfumigated fruit attained uniform deep red colour when the acid solution is infiltrated by a vacuum (~1/3 atmosphere) or when detergent (~0.1% v/v) is added to the acid dip. When nonfumigated fruit are treated either with a high acid concentration (higher than 2 M) or for a longer time (more than 2 min) with the recommended (2 M) acid solution, the colour of the pericarp is always redder and uniform (Figure 2c). However, in all the cases described, except for the recommended treatment, some browning and/or softening of the aril occurs (Fuchs et al., 1993).

5 | POSTHARVEST HANDLING OF LITCHI FRUIT

5.1 | Techniques applied in the industry

The commercial postharvest handling of litchi varies with the nature of the market, with the biggest difference between fruit destined for a local versus an export market. For local short-distance markets, fruit are generally delivered by trucks or ships within 1–2 weeks of harvest. This occurs frequently among Asian countries and in other producing countries such as South Africa and Australia. For long-distance export markets, fruit are transported by air cargos or ships and can take up to 3–4 weeks or more. This is the case for litchi moving from Southeast Asia, South Africa, and Australia to major markets in North America, Europe, and Japan. These export markets can have additional requirements, such as required insect disinfestation protocols that place additional stress on the fruit and require procedures to minimize loss in quality. In both market types, the major postharvest issues relate three interacting causes of quality loss: mechanical injury, pericarp browning, and disease. In both cases, fruit are sorted and graded to meet market requirements whether to be sold in bunches or as single fruit, often in punnet with a plastic overwrap. Damaged, cracked, and split fruit is removed. In some areas, bird damage can be a major problem (Figure 4a).

During short-distance transport for the local market, the application of a cold chain is useful, with other treatments such as SO_2 fumigation and/or acid dip being applied if warranted by market conditions. When shipping to cold chain export long-distance markets, the use of plastic barriers with SO_2 fumigation and/or acid dip to preserve pericarp colour and prevent browning and decay is essential. Insect disinfestation (quarantine) requirements that may involve heat or cold treatments, or irradiation, are necessary for some export markets and are carried out before or during shipping. However, these disinfestation treatments cause stress and can have adverse quality effects on the fruit. The use of SO_2 treatment may be approved for the control of decay in some countries but not for cosmetic reasons to preserve pericarp colour (browning).

5.1.1 | Cold chain

Data from several studies have confirmed the effectiveness of low-temperature storage and high relative humidity in preserving litchi fruit quality (W. X. Chen et al., 2001;

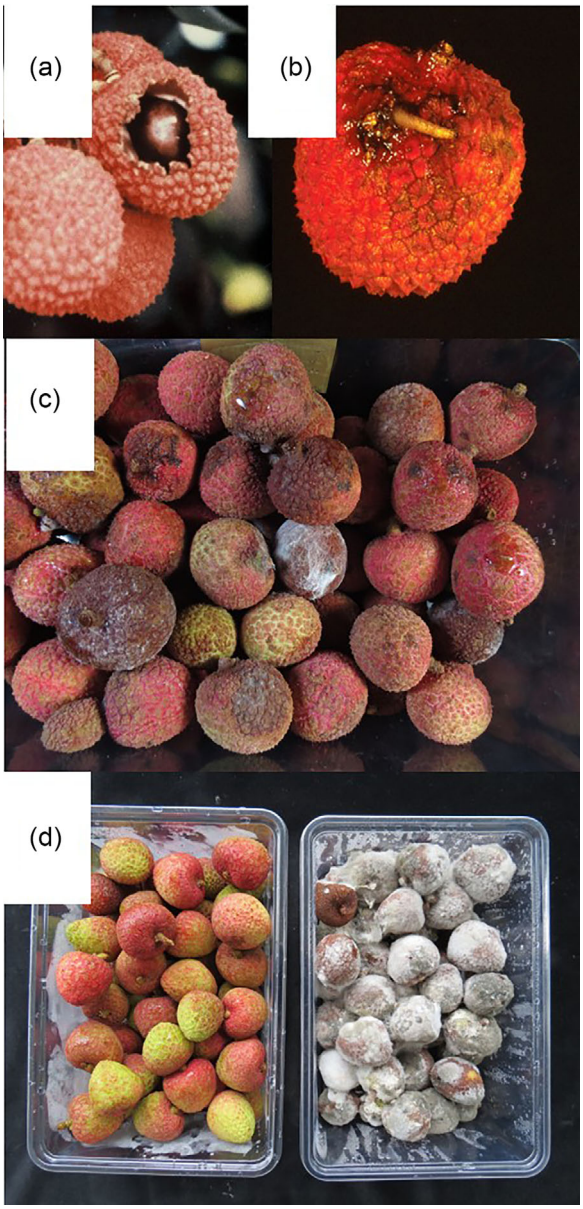


FIGURE 4 Litchi showing (a) bird damage common in ripe fruit, (b) fruit fly larvae emerging from fruit, larvae seen between the aril and pericarp cause little damage though fruit fly egg lay can lead to yeasty fermentation at the puncture wound, (c) mold due to *Colletotrichum gloeosporioides* on the fruit surface, and (d) miscellaneous bacterial saprophytic growth on fruit.

Hatton et al., 1966; South African Litchi Growers' Association Website 2020; Tongdee, 1998; Underhill, 1994). Storage temperatures of 10˚C for 7 days in sealed plastic bags (Hatton et al., 1966), 2–5˚C with plastic packaging (Underhill, 1994), sealed plastic punnets at 4˚C, for up to 2 weeks (South African Litchi Growers' Association Website, 2020) are reported. Other cooling treatments include; fruit in plastic bag with ice placed on top (with a 1 to 35—ice to fruit ratio) in a sealed polystyrene box (W. X. Chen et al., 2001), and hydrocooling followed by shipping at temperatures above 4–7˚C (Tongdee, 1998). The objective of these conditions is to have a satisfactory commercial control of browning. The thickness of the plastic wrap or bag varies from stretch wrap in the case of punnets to thicker bags (0.04–0.05 mm thick). Harvesting fruit in the cooler morning hours and keeping the fruit cool and in the shade, or the use of sprinkling the fruit with water to prevent drying out are also recommended in some situations (Tongdee, 1998).

An example of an integrated system with both local and export markets is in Taiwan. The local market is served in less than 5 days, while it takes 7–14 days for exported fruit to South East Asia. Fruit is harvested in the early morning, kept in the shade, and sent to the packing house as soon as possible. At the packing plant, fruit are forced air cooled at 5˚C with very high relative humidity and packed in punnets that are stacked in cartons. The packed cartons are then precooled before loading into refrigerated shipping containers and shipped at 5˚C. Fruit destined for the Japan market need a vapor heat combined with low-temperature disinfestation treatment, which raises the fruit core temperature above 46.2˚C and is maintained for 20 min. The fruit is then cooled to below 2˚C fruit core temperature for 6 h and maintained at that temperature for 42 h before shipment at 5˚C. After this treatment regime, the fruit pericarp quickly turns brown when moved to room temperature after transportation.

5.1.2 | Fumigation of sulfur dioxide (SO_2) and combinations with other treatments

SO_2 fumigation

The SO_2 fumigation procedure was developed in the early 1980s (Swarts, 1983) and is commercially used and has been continuously improved (De Jager & Korsten, 2003; Lemmer & Kruger, 2000a; Sivakumar et al., 2010; Swarts, 1985; Tongdee, 1994). This fumigation treatment prevents the browning of the pericarp when exposed to chilling conditions or desiccation. The fruit can last up to 5 weeks at 1˚C after fumigation, while the untreated fruit only lasts 2 weeks at 4˚C (South African Litchi Growers' Association Website, 2020). This treatment is used in many countries, including South Africa (Swarts, 1985), Thailand (Tongdee, 1998), Israel (Zauberman et al., 1991), and Madagascar (Wermund, Goyard, Jahiel, et al., 2014). Wermund et al. (2014) reported that in Madagascar, sulfuring litchis is currently the only commercially viable means to control decay and retain colour, and it is the sole legal postharvest method according to current European legislation.

A concern with this treatment and the use of metabisulphite pads is the SO_2 residues remaining in edible aril (Kremer-Köhne, 1993; Paull et al., 1998). The European Union has a maximum concentration of 10 ppm in the aril requirement (Ducamp-Collin, 2001; Sivakumar et al., 2010). In the United

States, sulfur dioxide use on fresh fruit and vegetables is approved for some commodities as a pesticide to control diseases such as on table grapes, and this is controlled by the Environmental Protection Agency (EPA); however, it is not approved by the Food and Drug Administration (FDA) for cosmetic purposes such as controlling browning (FDA, 1986). SO_2 residues in table grapes must be <10 ppm total SO_2. This ban by the FDA was in response to numerous cases of sulfite-induced asthma that occurred after the ingestion of green or fruit salads treated with sulfites.

In early protocols, the fruit were placed in a closed container or room, and 100–150 g sulfur per cubic meter of air was burnt (Swarts, 1983). In South Africa, fruit are now placed in an airtight container and fumigated for 20 min with 0.6 g of sulfur/kg of fruit (De Jager & Korsten, 2003), or 50 min (Wermund, Goyard, Jahiel, et al., 2014), or 500 g of 99% SO_2 per metric ton of fruit for 30 min (Lemmer & Kruger, 2000a). Other protocols involve 100 g of 90% sulfur powder per m^3 of fruit at 25–28°C for 20 min with no humidity control (Holcroft & Mitcham, 1996; Sivakumar et al., 2010). In Thailand, a standardized procedure uses gaseous SO_2 (Tongdee, 1994), with a 5:1 ratio between free space volume (milliliter or liter) of the chamber and the weight of the fruit (gram or kilogram). The fumigated fruit absorbed 30%–60% of the sulfur dioxide applied. Maximum efficacy in controlling browning is obtained when the whole fruit residues are 200–350 ppm immediately after fumigation with the residues concentrated in the pericarp, and aril levels are very low. In this protocol, the facility must have a scrubbing system to reduce the exposure of the operator and environmental release.

The extent of sulfite residues in the pericarp and aril is highly dependent on the condition of the fruit (cultivar, maturity, and pericarp damage) and the treatment and storage conditions (relative humidity, temperature, fruit load, SO_2 concentration, and duration of treatment). The Hong Huai litchi fumigated at the optimal rate had SO_2 pericarp residues immediately after fumigation from 1200 to 2000 ppm, while the pericarp in Khom was much higher (Tongdee, 1994, 1998). These residues in the pericarp rapidly decreased within the first 2 days after fumigation. Pericarp sulfur dioxide residues of 150–500 ppm are required to maintain fungistatic levels during the marketing period and avoid recontamination by *Penicillium* sp. (Tongdee, 1998). The sulfur residues in McLean's Red are considerably higher than in HLH Mauritius, especially when incorporating an acid dip. In addition, more mature McLean's Red fruit tend to have unacceptably high levels of aril sulfur dioxide residue compared to less mature fruit. High ambient temperatures combined with low humidity lead to an increase in aril sulfur residues, especially when fruit are left overnight before fumigating (Lemmer & Kruger, 2000a). The residues in aril are higher following treatment, and the level declines with 4 weeks of storage (Kremer-Köhne, 1993). In 79% of the samples analyzed, the SO_2 residues in the pulp exceeded the tolerance level of 10 ppm after storage, while only 22% of the samples fell into this category. Schoeman et al. (2004) also reported that overmature McLean's Red litchis had significantly higher SO_2 residues in the aril of the fruit. Different producers had significantly different SO_2 residues in litchi aril, though using the same procedure. The degree of microcracking of the pericarp may play a role in aril sulfur residues, and this could be influenced by the preharvest fruit growth environment.

Swarts (1985) suggested that sulfur fumigation did not adversely affect aril eating quality. When residues are high, the taste of the fruit can be altered with reports of higher titratable acidity (Lonsdale & Kremer-Köhne, 1990; Tongdee, 1994). Negative effects on soluble solid content (SSC)/titratable acidity (TA), taste, and membrane integrity (Sivakumar & Korsten, 2010) along with loss in flavour of SO_2 fumigated fruit and decrease in turgidity in the aril are also reported (Y. M. Jiang et al., 2006). Another adverse impact of this fumigation is that the bleached pericarp turns pink (Zauberman et al., 1990), and this is not as attractive as red. When excess sulfur is used, the fruit turns yellow or pale green and fails to redden (Holcroft et al., 2005). Sulfur dioxide can also cause phytotoxic symptoms with irregular brown lines or patches on the underside or interior of the rind that occurs when fruit are fumigated at a very low dosage (Tongdee, 1998) and is only apparent on the second day (Tongdee, 1992). Increased pericarp weight loss and microcracking have been observed (Sivakumar & Korsten, 2004), showing that SO_2 fumigated fruit is not popular on the Chinese market (Y. M. Jiang et al., 2006). The SO_2 treated fruit destined for Asian markets have not been well received (Tongdee, 1998). Furthermore, the rot problem could persist in fumigated fruit (Lemmer et al., 2001; Schoeman et al., 2008, 2014).

In SO_2 fumigation, though simple in concept, is greatly influenced by fruit cultivar and the fruit physiological state and the conditions of treatment (Tongdee, 1998). Residues in the aril being less than 10 ppm are of concern and may not always be achievable in practice. Different analytical methods for SO_2 residues lead to some uncertainty in interpretation (Wermund, Goyard, Reeber, et al., 2014). Alternatives to replace or improve SO_2 treatment and maintain fruit appearance are a continued area of active research (Sivakumar et al., 2010).

Acid dip after SO_2 fumigation

Zauberman et al. (1990) developed acid dips after SO_2 fumigation to address the pink pericarp and recover redness from the pericarp. If the fumigated bleached fruit was dipped in low PH solutions, redness was recovered with no adverse effect on fruit quality. Dilute HC1 at PH 0.5 or 1.0 was the best way to recover red pericarp. The degree of red recovered was determined by both PH and the duration of exposure. Acid treatment if done with SO_2 fumigation must also be applied

before the pericarp turns brown (Zauberman et al., 1991). The fruit can be treated with 1 N HCI (1.2% for 10 min) immediately after gaseous SO_2 fumigation (Underhill, Bagshaw, et al., 1992). The treated litchi fruit are uniformly red and stable without browning. Therefore, acid dip after SO_2 fumigation is commercialized in South Africa and Israel (Fuchs et al., 1993; Lichter et al., 2000; Sivakumar et al., 2010; Underhill, 1994). The SO_2 fumigated fruit takes 3–5 days to turn pink. Fruit airfreight to market is often additionally treated with organic acids after sulfur fumigation to allow for a quicker return of the reddish pericarp (South African Litchi Growers' Association Website, 2020).

Fruit treated with an acid dip after SO_2 fumigation can cause fungal infections during storage and shipping (Fuchs et al., 1993). Dipping litchi fruit in HCl eliminates the infection caused by common opportunistic fungi but not *Penicillium* species that tolerate low PH (Lichter et al., 2004). If acid dip after SO_2 fumigation treatment, the application of Sportak (prochloraz 0.2%) separately or in combination with acid can effectively retard the incidence of fungal infection (Fuchs et al., 1993). Additionally, brown patches inside the pericarp occur when fruit are acid dipped without SO_2 fumigation (Fuchs et al., 1993). Acid dipping after SO_2 fumigation has been shown to increase SO_2 residues (Lemmer & Kruger, 2000a), and if not done correctly can cause off-flavor, and the pericarp will have acid injury that is degraded, soft, and weak (Tongdee, 1998).

SO_2 fumigation and sulfur sheet package

Sulfur sheets are used to reduce fruit rot during storage and shipping to supplement SO_2 fumigation and reduce the concentration used in SO_2 fumigation. This technology was developed in the 1980s (Lichter et al., 2008; Nelson & Ahmedullah, 1976). There are many names for these sulfur sheets, including sulfur pads, slow-release sulfur dioxide sheets, and sodium metabisulfite impregnated sheets (SMS sheets). The pads are made by encapsulating sodium metabisulphite between two thin plastic sheets. SO_2 gas is generated by the reaction between sodium metabisulphite and moisture produced by the fruit (Wermund, Goyard, Jahiel, et al., 2014).

Schutte et al. (1990) reported that using two SMS sheets one on either side of the litchi within a polyethylene bag gave 100% control of decay, and only 2% pericarp browning occurred after 21 days of storage at 3.5°C. Others found that a single sheet at the bottom of the carton significantly reduced the incidence of fungal infection of previously fumigated SO_2 fruit and did not increase SO_2 residues in fruit (Schoeman et al., 2008). Care is necessary in the concentration of SO_2 used during fumigation and the dosage and placement of the sheet (Schoeman & Kruger, 2004). The sulfur sheet, placed at the bottom of cartons containing fumigated litchi fruit, reduces fungal infections during the mid to late stages of storage at 1°C for 30 days. The maximum limits for SO_2 residues of the European Union (10 ppm in aril) should not exceeded. The use of a well-ventilated carton gave better results than poorly ventilated cartons (Schoeman et al., 2009, 2014).

Fumigating with the reduced amount of sulfur concentration (300 g t^{-1} at 40 min) compared to the control (600 g t^{-1} at 50 min) with sulfur pads gave lower final aril residues (<10 ppm), decay, and colour retention (Wermund, Goyard, Jahiel, et al., 2014). The pads were placed only on top of the litchi in a cardboard carton. Different cultivars may require different active concentrations of SO_2 to be used (Schutte et al., 1990). These sheets are currently used by certain South African and Madagascan exporters (Dodd et al., 2010). In South Africa, depending on the market, the fruit is packed in 2-kg cartons or smaller plastic punnets. For long-term storage, litchi cartons can be packed with a slow-releasing sulfur dioxide sheet on top of the fruit (South African Litchi Growers' Association Website, 2020).

SO_2 fumigation and controlled atmosphere

The quality of late-harvested fruit is poorer than early- and mid-season fruit. The incidence of rot is also higher in late-harvested fruit after regular fumigation and storage (Lemmer et al., 2001). Controlled atmosphere (CA) storage after SO_2 fumigation reduces fruit rot (Lemmer & Kruger, 2000b). The fungal growth on "HLH Mauritius" fruit was retarded when stored at 1°C in CA than with the commercial standard regime. However, the effect is negated during the ensuing shelf-life phase, and the SO_2 residues were higher than those of the controls. Cultivar differences are found with CA storage that significantly reduces fungal infection, while the proportional increase in sulfur residues was less pronounced than in "HLH Mauritius" (Lemmer & Kruger, 2000b). In the study by Lemmer et al. (2001), more than 35% of fruit were infected by fungi during storage after SO_2 fumigation and cold storage. Fruit was not infected if they were kept in CA (1% O_2:12% CO_2). However, the SO_2 residues in these fruit was higher, indicating that SO_2 is less released from the fruit under CA. A proportion of fruit is currently exported under CA, especially late-season fruit (Dodd et al., 2010).

5.1.3 | Quarantine disinfestation treatment

Several litchi-importing countries require an insect disinfestation (quarantine) treatment before importation. Treatment must be completed before import. The treatments that are currently approved, depending on the country, include low-temperature and vapour heat treatments, irradiation, or a combination of both. Treatments vary by importing countries and according to the different insect pest species in the exporting country. For example, since litchi is considered a fruit fly host (Figure 4b), the United States requires an approved

treatment for fruit from fruit fly-infected areas before entering the United States. Currently approved treatment includes irradiation, heat, and cold treatments (Follett & Neven, 2006; Roberts & Follett, 2017). In some cases, no treatment is necessary from declared fruit-fly-free zones such as in Mexico, Israel, South Africa, and China. Litchi fruit exported to the United States from China requires cold treatment. Consignments must also be free from soil, weed seeds, and extraneous material.

For irradiation, fruit must be treated with a minimum 300 Gy dose, with a dose of at least 400 Gy if other pests besides fruit fly are present. For heat treatment, the litchi core temperature must be maintained at 45˚C for 30 min, and for cold treatments, the fruit core temperature must be maintained at 1˚C for 14 days. In all cases, the shipment must include a phytosanitary certificate. The details of the treatments are found in the USDA-APHIS treatment manual at https://www.aphis.usda.gov/import_export/plants/manuals/ports/downloads/treatment.pdf.

The exporting country must draft disinfestation treatment procedures according to the regulations of the importing country. For example, in the export of Taiwan litchis to the United States, the fruit must receive a cold treatment in which the core temperature must be below 0.99˚C for 17 days, or 1.38˚C for 20 days. This treatment must be applied before entering the United States. Since the shipping time from Taiwan to the West Coast of the United States is usually more than 20 days, the cold treatment can be carried out in transit. For litchi exported to Japan and South Korea, a combination of vapour heat and low-temperature treatment is approved. The fruit is subject to vapour heat, and the core of the temperature of the fruit must be above 46.2˚C and maintained for 20 min. The fruit is then cooled, and the temperature of the fruit must be lowered to below 2˚C in 6 h and maintained for 42 h. The disinfestation treatment of litchi exported to New Zealand or Australia can be either heat treatment or cold treatment. The temperature and time of the treatments vary by country.

Heat or cold treatments used for disinfestation may cause damage or induce chilling injury to litchi fruit (Follett & Neven, 2006). Many studies have been conducted, trying to reduce this damage. Jacobi et al. (1993) reported that litchi fruit Tai So (Dazao) and Wai Chee (Huaizhi) tolerated vapour heat treatment, where the core temperature is 45˚C for 42 min, and 2 weeks at 5˚C without a significant reduction in fruit quality. Kwai May Pink (Guiwei) does not tolerate treatment. Earlier reports had shown that storage at 1˚C for 12 days or hot water treatment at 49˚C for 20 min leads to pericarp browning (Paull et al., 1995). The hot water treatment combined with the sulfur dioxide treatment prevented the damage, with residue in the edible aril on a fresh mass basis of less than 5 ppm. The fumigation load factor significantly influenced pericarp and aril sulfite residues, and at 53 kg m^3, aril sulfite residues were 1 ppm (Paull et al., 1998). Litchi fruit are treated with immersion at 49˚C for 20 min, or irradiation treatment at a minimum absorbed dose of 400 Gy, is required for export from Hawaii to the mainland United States. After cold storage, the fruit treated with hot water immersion were darker and less intensely coloured and were rated unacceptable, while the irradiated fruit were acceptable. It was suggested that irradiation is superior to immersion as a quarantine treatment based on the maintenance of fruit quality (Follett & Sanxter, 2003). Recently, the use of paraffinic oil as an insect disinfestation treatment has been studied. Revynthi et al. (2020) reported that postharvest dips in STYLET@ paraffinic oil solutions for 60 s resulted in complete disinfestation of the litchi fruit of crinose mite (*Aceria litchi*) without adverse effects on the colour of the pericarp.

5.2 | Research approaches and techniques

5.2.1 | Preserving quality

Postharvest litchi research can be divided roughly into two types: the development of practical technology and physiological research. When developing practical technology, such as finding replacement for SO_2 and acid dip treatments, research needs to incorporate simulated transport and storage conditions and evaluation of quality criteria relevant to the market. These commercial market expectations can vary depending on consumers' desires and familiarity with the commodity. This commercial aspect has led to considerable physiological research as it relates to the effects on the fruit of various treatments that often add additional stress.

Chemical treatment

Acid dip can prevent the browning of litchi fruit peel (Zauberman et al., 1990), although it can cause brown patches on pericarp (Fuchs et al., 1993; Tongdee, 1998) and disease caused by *Penicillium* spp. (Lichter et al., 2004). Data suggest that the brown patches on the pericarp may be due to uneven intrusion of acid, and this is supported by the observation that SO_2 fumigation before the acid dip increases membrane permeability and prevents the occurrence of brown patches (Fuchs et al., 1993). Hot water brushing in combination with acid dip treatment was developed (Lichter et al., 2000) to replace the SO_2 fumigation step. In this treatment, litchi fruit are sprayed with hot water while being brushed in a revolving drum, after which the fruit are subjected to HCl treatment. These fruit maintained a uniform red color after 3 weeks of storage at 1.5˚C and 3 days at 20˚C. This outcome is similar in fruit treated with an acid dip after SO_2 fumigation. Dipping litchi fruit in HCl eliminates infection by common opportunistic fungi (Figure 4c) and selects for species that tolerate low PH. Adding prochloraz(9N-propyl-N-[2-(2,4,6-trichlorophenoxy) ethyl] imidazole-1-carboxamide) in acid

dip can effectively retard fungal infection (Lichter et al., 2004). Also, Ketsa and Leelawatana (1992a) found that an H_2SO_4 dip is better than HCl for red color retention. They recommended a PH 0.2 H_2SO_4 dip for 15 min. Extensive research has been done on the development of acid-based treatments to retain litchi's red pericarp. In all cases, the protocols have been refined to improve handling and reduce sulfur residues, avoid off-flavors, and retain pericarp color (Dodd et al., 2010).

The sodium metabisulphite dip followed by HCl dips gave good results in the color, taste, and disease control of the litchi fruit after 28 days of storage at 1˚C and 3 days on the shelf (Duvenhage, 1993) and delivered fruit of superior quality to the SO_2 fumigation-treated fruit only (Duvenage et al., 1995). Among many different treatments to maintain fruit marketability, a combination of potassium metabisulfite and Vapogard treatment was most effective, reducing pericarp browning, disease, and retaining fruit firmness after 21 days of storage at 1˚C and 2-day shelf at 18˚C (Sivakumar et al., 2005). Precooling fruit before dip in 0.6% sodium metabisulphite for 10 min, air drying then a dip in 2% HCl for 5 min then packing in perforated low-density polyethylene (LDPE) bags as an modified atmospheres package (MAP) treatment gave the best results (Neog & Saikia, 2010). The treated fruit showed lower PPO activity, high anthocyanin content, low pericarp browning, and had 9 days of postharvest life versus 2 days in the control. Liang et al. (2012) found that dip of litchi fruit in 6% sodium metabisulfite solution followed by 1.1 M HCl delayed pericarp browning and effectively reduced decay. No sulfite residue was detected in the aril. However, the incidence of decay increased greatly when half the dose (3%) of sodium metabisulphite is used, indicating that the control of sodium metabisulphite concentration is crucial in commercial practice.

Chitosan coating reduces the total microbial population on the fruit surface compared to other treatments (Sivakumar et al., 2005), though it did not retain fruit marketability when compared to a potassium metabisulphite/Vapogard dip. The fruit treated with a 1% chitosan solution had a lower respiration rate, aril temperature, PPO activity, and weight loss during 5 days of storage. Chitosan coatings show two different characteristics; the coating exposed to air was more uniform and closely packed like a barrier, while the other in contact with pericarp is rougher and has a better transport rate (B. Lin et al., 2011). The new chitosan formulation (Kadozan) reduces the fruit's respiration rate, delays the increase in membrane permeability, and maintains higher contents of anthocyanins and flavonoids contents. The coated fruit also has higher pericarp *L*, *a*, and *b* values and better maintains the TA, TSS, and vitamin C content in the aril. At ambient temperatures, these coatings had a lower browning index and disease index and had reduced fruit weight loss (X. Jiang et al., 2018). If first treated with thiabendazole, a chitosan coating similarly decreased browning and decay; weight loss; and delayed changes in anthocyanin, flavonoid, total phenolics, PPO activity, and partially inhibited the increase in POD activity (D. Zhang & Quantick, 1997). MAP and especially MAP plus chitosan coating retain fruit quality (De Reuck et al., 2009a) by preventing decay and browning while significantly reducing PPO and POD activity, maintaining membrane integrity, and anthocyanin content.

Chitosan coating in conjunction with organic acids (citric or tartaric) at different pHs has shown that the rate of browning of pericarp during storage parallels the rate of dehydration and pericarp pH. The lower the pH, the more total phenols and anthocyanin were retained (Joas et al., 2005). A pH 0.8 was better than pH 1.0 or 1.3, which gave more variable results. Acidic coatings reduced the surface pH from 5.0 to 3.3, which lasted throughout cold storage and maintained the red color, while with acid dips alone, the surface pericarp pH would eventually return to 4.8 (McGuire & Baldwin, 1998). Dipping the fruit in water immediately prior to treatment favored acid infiltration, suggesting that the response to the treatment is partially dependent on the pericarp water content (Caro & Joas, 2005). Fruit treated with 60% citric acid in 0.75% chitosan retained pericarp color for 21 days at 4˚C. A major issue with this treatment was its high viscosity and the long duration required for fruit drying after treatment (Ducamp-Collin et al., 2008). Other researchers have evaluated anti-oxidants such as ascorbic acid in conjunction with chitosan treatment and found slower browning of membrane leakage reduced pericarp PPO and POD activities and increased pericarp SOD and CAT activities with higher levels of aril AsA and GSH and lower amounts of H_2O_2 and MDA (D. Sun, Liang, et al., 2010). The decay rate was also lower. Coatings other than chitosan have also been evaluated. A polymer coating after SO_2 fumigation reduces water loss and the percentage of fruit colonized with *Penicillium*. However, the taste and juice TSS content are reduced by this coating (Oosthuyse, 2014). Organic acids (acetic, malic, citric, and oxalic acid) and inorganic salts (NaCl and CaCl2) have been evaluated for their in vitro inhibitory effects on POD and phenol oxidases, although they do not improve color retention or even favored pericarp browning (Reichel et al., 2017). Coating with 10% gum arabic significantly lowered browning index, weight loss, decay, and respiration rate (Sultan, 2014). Treatment of fruit with calcium nitrate followed by a dip in HCl gave promising results in colour and taste after storage (Duvenage et al., 1995).

There are numerous studies on coatings and chemical treatments other than those mentioned above. Many chemicals significantly reduce browning and have led to in-depth investigations of their physiological response including membrane stability, oxidation, and energy status. These factors, as discussed above, are closely related to pericarp browning. It is often found that a chemical treatment that effectively inhibits browning will usually maintain all or some of these

physiological factors within normal ranges, implying their interrelationship. Examples would be melatonin (G. Liu et al., 2020; T. Wang et al., 2020; Y. Zhang, Huber, et al., 2018), ACS (C. Y. Wang, Chen, et al., 2010), polyamines (Y. M. Jiang & Chen, 1995), gel of aloe vera (Ali, Khan, Nawaz, et al., 2019), L-cysteine (Ali, Khan, & Malik, 2016), methionine (Ali et al., 2018), sodium para-aminosalicylate (PAS-Na) (T. Li, Shi, et al., 2019), kojic acid (Shah et al., 2017), oxalic acid (X. Zheng & Tian, 2006), nitric oxide (Barman et al., 2014), salicylic acid and chitosan (Kumari et al., 2015), salicylic acid and isoascorbic acid (Kumar et al., 2013), salicylic acid (Pongen BAP) (D. Zhang, Xu, et al., 2018), ALA, thidiazuron (M. F. Li, Feng, et al., 2019), and citric acid combined with GSH (Y. Jiang & Fu, 1998).

Pericarp browning is a major cause of quality loss after harvest; the other cause is disease or saprophytic growth in the fruit pericarp (Figure 4c,d). Numerous disinfectants and other chemicals have been tested to address the decay problem. De Jager and Korsten (2003) tested nine fungicides and 18 disinfectants, and among these, the organic tin complex disinfectant (OA5 Dp) and the fungicide prochloraz gave the best results with SO_2 fumigation fruit in maintaining the colour of the pericarp and reducing decay and water loss. The lactic acid bacterium *Lactobacillus plantarum*, often associated with the plant microbiome, has been shown to be a biocontrol agent (Trias Mansilla et al., 2008). When litchi is sprayed with a suspension of this bacterium, there were reduced color loss, better maintenance cyanidin-3-rutinoside, total anthocyanin, and phenolic compounds (Martínez-Castellanos et al., 2011). Although the authors did not report the level of decay, they did present data showing survival and growth in the pericarp suggesting biocontrol via competition for space and nutrients competing with decay organisms. Immersion of litchi fruit in *Bacillus amyloliquefaciens* LY-1 culture broth led to fruit with less pericarp browning, fruit decay, and weight loss. The pericarp also had higher PAL and β-1, 3-glucandase activities often associated with disease resistance, and a higher content of disease-related lignin (Y. Wu et al., 2017). The treated fruit also had a higher content of aril TSS, TA, total soluble sugars, and vitamin C. Treatment of litchi with *Photorhabdus luminescens* Hb1029 effectively repressed the decay of litchi fruit, reduced browning index, and weight loss. It also increased the pericarp of POD, SOD, and CAT activities and increased the content of aril trehalose with a significant decline in pericarp MDA and H_2O_2. The treated fruit maintained higher TSS, TA, and vitamin C (D. Lai et al., 2020).

Controlled atmosphere environment

CA in combination with low-dose SO_2 fumigation has been commercially used. There are still many studies on the use of CA alone. Fruit quality is maintained in a CA environment, and 3%–5% O_2 + 5% CO_2 is recommended at 5–7°C (Paull et al., 2002); however, for commercial use, the fruit quality must also be maintained well after the CA storage phase into the retail period. The same CA storage protocol has been applied at 13°C with success (Y. M. Jiang & Fu, 1999b). Ali, Khan, Malik, and Shahid (2016) tested nine different combinations of O_2 and CO_2 with 1% O_2 + 5% CO_2, giving the best result by reducing weight loss, pericarp browning, membrane leakage, and MDA contents. Treatment also maintained aril TSS, TA, and AsA content and organoleptic quality. The pericarp CAT, SOD DPPH radical scavenging activities, total anthocyanins, and phenolic contents were maintained. In contrast, these CA storage conditions lowered the activities of PPO and POD.

Higher levels of CA (5% O_2 + 5% CO_2) were more effective in delaying anthocyanidin decomposition, preventing browning, and decreasing fruit decay than MAP (15%–19% O_2 + 2%–4% CO_2) or control (Tian et al., 2005). Fruit quality was maintained without any flavour changes after 42 days of storage at 3°C. Pornchaloempong et al. (1998) had previously reported that CA with 4% O_2 + 7.5% CO_2 was the best at maintaining the fruit quality of the three combinations tested. Treatment reduced decay and maintained pericarp colour for 4 weeks of storage plus 1 day at 20°C. However, Sivakumar and Korsten (2010) found that fruit stored in 7% O_2 + 3% CO_2 had a higher browning of the pericarp, PPO, POD activity, and loss of membrane integrity. CA with 17% O_2 + 6% CO_2 showed a good result, especially when combined with 1-MCP. These CA conditions (17% O_2 + 6% CO_2) plus 1-MCP were more effective in preventing browning, loss of red colour and AsA content, and retaining SSC/TA and taste. The treated fruit showed higher overall acceptance with lower PPO and POD activity, lower membrane leakage, and lower anthocyanin content during storage.

The browning was significantly retarded by holding the fruit in 50%–70% O_2 at 4°C (Techavuthiporn et al., 2006). When held at 90%, O_2 initially had the same inhibitory effect on browning but then accelerated the browning rate later in storage. These results were confirmed by Duan et al. (2011) who reported that pure oxygen significantly prevented pericarp browning and delayed the increase in membrane leakage. This storage atmosphere reduced lipid peroxides, induced the activities of antioxidant enzyme activities, and increased antioxidant capacity.

Modified atmosphere package

The results obtained with different concentrations of O_2 and CO_2 in CA storage show improvement by maintaining fruit quality. However, most CA systems are only economically viable when large quantities of fruit are being stored or shipped and are not easily implemented for air shipment, where MA is a more viable treatment. CA storage also requires considerably more technology and management skills. The results from the above CA studies are useful guidelines for developing MA storage regimes giving

starting values for desirable gas atmospheres. In MAP, another issue is the change in storage atmosphere when the fruit are moved from the low-temperature storage environment to retail display where the temperatures are higher with concomitant changes in O_2 and CO_2 concentrations in the MAP and the increase in respiration rate. These changes predicate that the fruit is kept at storage temperature well into the retail display phase such as 14˚C (Sivakumar & Korsten, 2006b) or lower.

In 1966, sealed polyethylene bags combined with refrigerated storage at 10˚C for 7 days resulted in satisfactory commercial control of litchi pericarp browning, while perforated bags were slightly less effective (Hatton et al., 1966). Kader (1998) in his review of published literature indicated that exposure to oxygen levels less than 1% and/or carbon dioxide levels greater than 15% induces off-flavours and a dull grey aril appearance (Kader, 1998). Flavor loss and loss of aril whiteness may occur when fruit are packed in a sealed PE bag and moved to a high temperature. If MAP is used, the fruit should be carefully sorted to remove any fruit with decay or obvious fly stings because the affected fruit may lead to mould on the adjoining fruit in the package (Sivakumar et al., 2010). It is frequently not cost-effective to open each MAP or wrapped punnet to remove decaying fruit leading to the loss of the whole package. During the last decade, considerable effort has gone into developing an MA-based export procedure, although few have achieved commercial export status (Dodd et al., 2010).

Combining MAP with other treatments to control browning and decay has shown potential. A hot water brushing and acid dip treatment of litchi fruit in laminated PE MAP bags to alter O_2, CO_2, and water transfer rates had less decay but poor taste after 4 weeks at 2˚C and 3 days at 20˚C when compared to fruit packed in bags with small holes (Pesis et al., 2002). CO_2 levels in the laminated MAP bag were 10%–15% for late harvest fruit, while only 0.2%–0.8% CO_2 was in the perforated bags, which had good taste but higher decay. The off-flavour in the MAP-packed fruit was likely due to higher levels of AA and ethanol.

Various plastic films have been evaluated. Litchi fruit wrapped in 35-μm biaxially oriented polypropylene (BOPP) films, widely used for food packaging, after being dipped in EDTA, created package atmospheres of 17% O_2 and 6% CO_2 within the BOPP-3 film that had the best final quality indicated by the retention of pericarp colour and excellent eating qualities after 34 days at 2˚C and 2 days at 14˚C. This film was better than the commercially used SO_2 treatment (Sivakumar & Korsten, 2006b). The efficacy of MAP, created with Xtend, a film with varying water vapour transmission rates, and BOPP was compared (Sivakumar & Korsten, 2006a). The BOPP MAP package had better results with reduced weight loss, colour deterioration, and decay and retained excellent eating quality after 34 days at 2˚C. The better results were attributed to higher RH and O_2 concentrations (17%). A hot water dip treatment at 50˚C for 2 min or at 55˚C for 1 min caused loss of pericarp colour, surface structure, and quality, which were not recovered with MAP storage.

The use of MAP has been confirmed in more recent studies. Ali, Khan, Malik, et al. (2019) reported that litchi fruit packed in MAP bags (Xtend StePac), stored at 5˚C, exhibited reduced decay and browning index. Fruit in these MAP packages had lower PPO activity and delayed superoxide anion production, MDA, H_2O_2, and membrane leakage with higher retention of anthocyanin. The aril of these MAP stored fruit had higher TSS, AsA content, and TA, with lower POD activity. The sensory quality, total phenolic content, radical scavenging activity, SOD, CAT, and APX activities of these MAP stored fruit were higher. Differences in responses can be expected due to the difference in O_2, CO_2, and water transmission rates of the different films at different temperatures (Mangaraj et al., 2009). Tian et al. (2005) did not find a better pericarp browning and decay control in MAP created with a 0.03-mm thick polyethylene film bag with 15%–19% O_2 and 2%–4% CO_2 than in the control, while a CA treatment with 5% O_2 and 5% CO_2 was more effective than the MAP.

The addition of 1-methylcyclopropene (1-MCP at 300 nL L^{-1}) to MAP made with BOPP gave better control of pericarp browning than MAP alone after 14 and 21 days of storage (De Reuck et al., 2009b). The pericarp with combined treatment had reduced PPO and POD activity, membrane leakage, and retained anthocyanin content. Higher concentrations of 1-MCP led to higher membrane leakage, pericarp browning, PPO, and POD activity.

Bacillus subtilis in a combination of MAP was tested by Sivakumar et al. (2007). A combination of *Bacillus* and MAP made with a polypropylene (PP) film gave the best results, controlling decay and browning of the pericarp during storage at 14˚C. Less than 1% of the fruit rotted or went brown with *B. subtilis* and PP film MAP in 11.3% absence of the *B. subtilis* 11.3% showed decayed. The atmosphere of MAP was ~14% O_2 and ~5% CO_2 after 14 days at 2˚C and 2 days at 14˚C. A MAP made with LDPE had ~3% O_2 and ~10% CO_2, the fruit showed decay and browning, and *B. subtilis* did not survive but survived in the PP MAP bag at 2 and 14˚C. A BOPP-1 MAP with *B. subtilis* developed 16% O_2 and 6% CO_2 also showed promise in controlling decay, retaining color and overall quality after 18 days at 2˚C and 2 days at 14˚C. BOPP-2 was less effective with 5% O_2 and 8% CO_2, even combined with *B. subtilis*, which did not survive well (Sivakumar, Arrebola, et al., 2008).

5.2.2 | Disease control

The incidence of disease

After pericarp browning, postharvest decay is one of the main problems facing commercial shippers. Microorganisms are important causes of fruit rot (Table 3). Pathogens that

TABLE 3 Numerous postharvest diseases do occur, and most have their origins preharvest. Good field sanitation and culling of fruit that show fruit piercing insects, cracks, and sun-scorch are effective in minimizing postharvest losses (Coates et al., 1994; Paull et al., 2014).

Group	Organism
Algal	None reported
Fungal	*Alternaria* spp.
	Aspergillus spp.
	Colletotrichum gloesporiodes (anthranose)
	Cylindrocladium scoparium (white molud)
	Geotrichum candidum (sour rot)
	Lasiodiplodia theobroma
	Penicillium spp. (green and blue moulds)
	Peronophythora litchi (fruit rot or downy blossom blight)
	Pestalotiopsis spp.
	Phoma epicocina
	Rhizopus oryzae
	Various yeasts
	Stem-end rots caused by a number of organisms (*Botryodiplodia theobroma*, *Phomopsis* spp., and *Botryosphaeria* spp.)
Insects	Various tephritid fruit flies
	Cryptophlebia peltastica litchi fruit moth
	Thaumatotibia leucotreta false codling moth

cause litchi fruit decay include *Alternaria* sp., *Aspergillus* sp., *Botryodiplodia* sp. *Colletotrichum* sp., and various yeasts (Koul & Taak, 2017).

Anthracnose (most commonly *Colletotrichum gloeosporioides*) is a common postharvest disease of litchi fruit. The initial infection occurs in the field, with subsequent growth and disease development occurring as the fruit ripens during storage and transportation. Only *C. gloeosporioides* causes the disease in the field and laboratory (Martínez-Bolaños et al., 2015). In Guangdong, up to 85%–100% of the fruit may be infected in the field, and thus it is the most important factor in causing the rot and browning of the fruit during storage and transportation (A. Liu et al., 2005). Similarly, high levels of pericarp infection (65%–90% of fruit) occur, beginning 20 days after initial fruit set (X. Li et al., 2005). The symptom of anthracnose begins to appear on the third or fourth day after harvest with a disease incidence of 83%−100%, 9 days after harvest. Anthracnose-infected fruit have higher respiration and ethylene production rates, higher pericarp MDA content, accelerated browning and decay, and shorter storage life (X. Li et al., 2006; A. Liu et al., 2006), and Litchi fruit inoculated with common anthracnose species (*C. gloeosporioides)* show higher respiration rate and ethylene production; increased rate of production of pericarp superoxide radical anion; MDA content; pericarp PPO, POD, and PAL activities; and decreased activity of SOD. It confirms that anthracnose increases the rate of senescence, browning, and decay of litchi (X. Li et al., 2006; J. Liu et al., 2006). Fruit rot caused by inoculation with *P. litchi* shows a similar physiological response (L. Zheng et al., 2019) with a higher respiration rate and ethylene production, increased pericarp levels of superoxide radical anion and MDA content, higher PPO and PAD activity, and reduced SOD activity (J. Liu et al., 2006). *Colletotrichum* sp., *Pestalotiopsis* sp., *Fusarium* sp., and *Lasiodiplodia* sp. can be isolated from the fruit pericarp showing symptoms of anthracnose (Martnez-Bolaos et al., 2015).

The predominant filamentous fungal genus isolated in South Africa is *Phomopsis* spp. (De Jager et al., 2003). Other prevalent postharvest pathogens in South Africa, in addition to *Phomopsis* sp., include *Pestalotiopsis guipinii*, *Trichoderma harzianum*, *Alternaria alternata*, *Lasiodiplodia theobromae*, and *Dothiorella* sp. Less prevalent pathogens are *Fusarium oxysporum*, *C. gloeosporioides*, *Rhizopus stolonifer*, *Penicilium expansum*, *Phoma* spp., and *Aspergillus niger*. Nonpathogenic fungi such as saprophytes found to readily colonize decaying litchi fruit included *Cladosporium* spp., *Nigrospora* spp., *Gliocladium roseum*, *Periconia cookei*, *Acremonium* sp., and *Penicillium* spp. Some bacterial species have also been isolated from decaying litchi fruit.

Fruit infection by microorganisms, such as *Aspergillus*, *Penicillium*, and *Rhizopus*, occurs during and after harvest with entry through pericarp wounds, whereas *Botryodiplodia* infects fruit either in the field or through the cut stem end during harvest and handling (Y. Jiang et al., 2003). The following genera can cause rot in both wounded and unwounded litchi fruit: *Phomopsis* spp., *Phoma* spp., *Colletotrichum* spp., *Alternaria* spp., *Dothiorella* spp., *Lasiodiplodia* spp., *Fusarium* spp., *Stemphylium* spp., and *Curvularia* spp. (Coates et al., 1994).

The importance of different organisms varies by region of production and postharvest practices. In northern Thailand, Sittigul et al. (1994) reported that *Cladosporium* sp. and *Fusarium* sp. were the fungi most detected during storage. While in South Africa, De Jager et al. (2003) gave anthracnose and *Phomopsis* spp. and *Penicillium* spp. (Jacobs & Korsten, 2004). Different postharvest handling practices led to a different spectrum of species; *A. alternata* and *Cladosporium* spp. were the main fungi in MAP made of BOPP-1, which had a higher O_2 concentrations, while *Candida*, *Cryptococcus*, and *Zygosaccharomyces* were the predominant yeasts in MAP made of BOPP-2, with a lower concentration of O_2 (Sivakumar, Arrebola, et al., 2008). *Penicillium* species can colonize almost any surface, from fruit to packhouse walls and air conditioning systems, leading to cross-contamination with at least 14 different *Penicillium* spp. have been identified (Jacobs & Korsten, 2004). Lonsdale and Kremer-Köhne (1990) found that different wrapping materials, such as Everfresh, Vitafilm, and plastic, significantly increase decay development.

Disease control

Treatment with hot water or hot water with chemicals to reduce disease has been studied since the 1960s. Swarts and Anderson (1980) reported good results in controlling mould growth by dipping the fruit for 10 min in a suspension of dicloran plus benomyl, preheated to a temperature of 52˚C. A dip in hot benomyl (0.05% at 52˚C for 2 min), followed by packing the fruit in punnets and overwrapping with a "cling" PVC film (0.01 mm thick) controlled rot, browning, and loss in weight at temperatures of 20–30˚C (Scott et al., 1982). Cultivar differences have been reported for these types of treatments, with hot benomyl (48˚C, 1–3 min and 50˚C for 1–2 min) being best for disease control and most acceptable fruit appearance in Tai So (Dazao), Kwai May Pink (Guiwei), and Wai Chee (Huaizhi), while a treatment of 52˚C for 2 min was unsuitable for cultivar Bengal (a seedling selection) (Wong et al., 1991). This treatment (500 ppm benomyl, 52˚C for 2 min) gives good control of both sides of the pericarp than stem-end lesions (Sittigul et al., 1994). A prochloraz dip (250 ppm) for 10 min effectively controls decay, while a hot benomyl dip (500 ppm at 52˚C, 2 min) was not effective (Lonsdale & Kremer-Köhne, 1990). A combination of hot benomyl (50 or 52˚C) and prochloraz treatments effectively controlled postharvest disease lesions (*A. alternata*, *Phomopsis* sp., and other fungi). The fungicides imazalil and iprodione have not given acceptable control (Coates et al., 1994). De Jager and Korsten (2003) reported that prochloraz and a disinfectant, OA5 Dp (organic tin complex disinfectant), demonstrated superior efficacy to SO_2 fumigation in preserving general fruit marketability. Benomyl is a broad-spectrum fungicide; however, due to toxicological concerns, in the United States, registration and thus its use were cancelled at the manufacturer's request (Pearson & Miller, 2014).

Sulfur dioxide fumigation has been used as a commercial practice and was approved to inhibit pericarp browning and retard fruit decay (Tongdee, 1998; Underhill, 1992; Wermund, Goyard, Jahiel, et al., 2014), but the decay problem persists (Lemmer & Kruger, 2000b; Schoeman et al., 2014). After SO_2 was fumigated, 10.5% of the fruit show decay after 18 days at 2˚C followed by 2 days at 14˚C (Sivakumar et al., 2007). The use of a sulfur dioxide sheet in the packing box can effectively reduce fruit decay in SO_2 fumigation fruit (Schoeman et al., 2008; Wermund, Goyard, Jahiel, et al., 2014). The CA condition during transportation is also effective in reducing the disease of SO_2 fumigated fruit, especially late-harvest fruit (Lemmer & Kruger, 2000b; Lemmer et al., 2001). To limit the sulfur dioxide residues in the aril, from sulfur dioxide slow-release pads in the carton, they have been evaluated and give good disease control. The pads do cause pericarp bleaching, and *Penicillium* sp. do colonized incompletely fumigated fruit. Sulfur dioxide fumigation provides excellent control of *Colletotrichum* sp. and *Alternaria* sp., although treated fruit are highly susceptible to colonization by *Penicillium* sp. (Coates et al., 1994). *Penicillium* sp. is the only fungus that develops on the pericarp after storage in acid-dipped fruit after SO_2 fumigation or hot water brushing. Prochloraz as a separate application or in combination with acid treatment effectively retards *Penicillium* infection (Fuchs et al., 1993; Lichter et al., 2004). Fumigation with SO_2 followed by dip of fruit in HCl containing prochloraz is the standard treatment of litchi fruit in Israel (Lichter et al., 2000). Fruit treated with sorbic acid, applied after hot water brush and acid dip, or combined with acid treatment after SO_2 fumigation, were significantly less prone to decay by *Penicillium* (Z. Zhang, Dvir, et al., 2005).

Continued concerns about the use of chemical fungicides and their residues efforts have focused on physical treatment such as hot water. Among the many combinations of hot water treatments, the most effective hot water dip was 1 min at 52˚C, which slowed the rate of rot development by ∼15%. A hot water spray is equally as effective as a hot water dip, though only half as effective as a hot benomyl dip possibly due to the lack of long-term protection in hot water treatment. Hot water treatments caused an immediate effect on pericarp color, with a positive linear relationship between dip time at 52˚C and color, indicating heat stress on pericarp cells (Olesen et al., 2004). Irradiation of fruit to control decay has been evaluated, and 200 Gy does reduce mould growth to about a third of the control with higher doses (500 Gy) giving almost complete control. Low doses (50 Gy) caused significantly greater mold growth than the control due to possible phytotoxicity (Kramer & Kuhn, 1964). Currently, irradiation doses of 150–400 Gy are approved for phytosanitary treatment for several insects on litchi in Australia, Thailand, and the United States (Follett, 2009). A 300 Gy did not affect vitamin C, organic acid, or sugar content (McGuire, 1997; Mitchell et al., 1992) or taste (Follett & Sanxter, 2003); higher doses in fruit from the same family lead to injury (Wall, 2008). Previous research had shown that for fruit held at 25–29˚C, doses greater than 2000 Gy are required to control decay and mould, with doses greater than 500 Gy altering flavour and aroma and over 250 Gy lead to a darkening of the pericarp (Akamine & Goo, 1977). Recently, Pandey et al. (2013) recommended 1000 Gy to extend postharvest life without quality loss, though no impact on pericarp colour and decay was presented.

More recent efforts have led to an evaluation of the use of volatile organic compounds. L. Zheng et al. (2019) found that preexposure of litchi fruit to volatile organic compounds (VOCs) produced by *B. amyloliquefaciens* PP19, *B. pumilus* PI26, and *Exiguobacterium acetylicum* SI17 significantly reduced the severity of downy blight during 36–72 h post-inoculation. Two of the compounds selected from the VOCs, 1-(2-aminophenyl) ethanone and benzothiazole, showed inhibitory activity against both *P. litchii* in plates and downy blight on litchi fruit when the compounds were applied directly. *Rhizopus nigricans* was identified as the

main pathogen causing decay of litchi fruit during storage. Treatment of a composite antimicrobial coating containing cinnamaldehyde was found to be effective in controlling decay (Y. Yang et al., 2019).

Biocontrol agents also show promise. *Bacillus subtilis* in MAP made with PP or BOPP-1 effectively reduced fruit decay. The O_2 concentrations in MAP are high, 14% or 16% in MAP made with PP or BOPP-1, respectively, and *B. subtilis* survived well under these conditions. The use of *B. subtilis* in MAP made with LDPE or BOPP-2 showed much less effectiveness. When O_2 concentrations in MAP are low (3%–5%), *B. subtilis* survival was adversely affected (Sivakumar et al., 2007, Sivakumar, Arrebola, et al., 2008).

6 | CONCLUSIONS

Rapid browning of the pericarp and decay of fruit after transportation poses great challenges in commercial marketing. This had been the driver of extensive studies on litchi postharvest handling technology and physiological responses. Several evaluated technologies have been successful, with the SO_2 treatments being the most used. This is done by SO_2 fumigation, followed by acid dip or CA storage and packaging with a sulfur sheet, after SO_2 fumigation. Limitations and adverse effects in the use of SO_2 are recognized, and alternatives are being pursued.

Efforts have been made to develop treatments to replace SO_2 fumigation (Sivakumar et al., 2010). Many treatments have been reported to have good effects, but not many have been commercially implemented. For commercial purposes, fruit must maintain good color and quality with low decay during the retail display phase at relatively high temperature. SO_2 treatment does achieve this goal and so far has been difficult to replace though not allowed in some markets. Acid dip is very effective in maintaining pericarp redness, but in addition to the problem of decay after transportation, brown patches on the pulp are also a problem (Fuchs et al., 1993; Tongdee, 1998). The appropriate acid drop after SO_2 fumigation effectively reduces this problem with little penetration of HCI into the aril. The pericarp color recovered is very stable (Underhill et al., 1994). These factors keep it in commercial use. Perhaps a greater understanding of the action of the mechanism of SO_2 that prevents the staining of the pulp with anthocyanin may help improve acid dip treatment.

There are many studies on the physiological responses to litchi pericarp browning after harvest. Recently, more reports indicate that the membrane's status is the key factor (Y. Jiang, Duan, et al., 2004). Many factors cause browning, including senescence, water loss, and chilling injury, all of which can result in damage to the membranes, which in turn results in the loss of membrane function in maintaining the cellular compartment and leakage. Maintenance of membrane function is affected by the membrane's antioxidant status of the membrane, energy status, and membrane lipid status (H. Liu et al., 2011; T. Wang et al., 2020; Yun et al., 2021; Y. Zhang, Huber, et al., 2018). Conditions or treatments favorable to maintaining membrane status all reduce browning. In recent studies, various aspects of physiological changes have been investigated. The results often show that a single treatment can cause various reactions; they interact with each other to produce the result, which accelerates or inhibits browning. For example, melatonin treatment delayed pericarp browning and reduced membrane leakage, which could be attributed to the maintenance of redox homeostasis by improving antioxidant capacity and modulating repair of oxidatively damaged proteins (Y. Zhang, Huber, et al., 2018) by modulating membrane lipid and energy metabolisms (T. Wang et al., 2020), and by regulating energy and proline metabolism (G. Liu et al., 2020). In another example, when comparing three cultivars, Jingganghongnuo exhibited the slowest changes in the browning indexes, and it had the highest content of antioxidants such as total phenols and anthocyanins; the lowest activities of ANT, LAC, PPO, POD, and PAL; the highest expression intensity of the metabolic-related ATP genes LcATPb, LcSnRK2, LcAAC1, and LcAOX1 (Tang et al., 2020).

Inhibition of browning and maintenance of red colour by SO_2 or acid dip treatment is due to direct chemical action on anthocyanin and does not appear to involve membrane integrity. Although SO_2 or acid dip treatment increases membrane leakage, it can still inhibit browning or maintain the red colour of litchi pericarp for a long time.

AUTHOR CONTRIBUTIONS

Chao Chia Huang: Conceptualization; writing—original draft; writing—review and editing. **Robert. E. Paull**: Conceptualization; project administration; writing—original draft; writing—review and editing. **Tsu-Tsuen Wang**: Writing—original draft; writing—review and editing.

ACKNOWLEDGMENTS

The authors wish to thank the SA Litchi Farmer Association for their support for the articles. Dr. Paull was supported in part by the US Department of Agriculture, National Institute of Food and Agriculture, under an agreement 58-2040-5-010 through the Agriculture Research Service and Hatch Project H862. The authors greatly appreciate the help of Dr. Ian Warrington in editing the earlier version of this review. His feedback and critical evaluation of the draft are greatly appreciated by the authors.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Robert E. Paull https://orcid.org/0000-0002-9733-9371

REFERENCES

Akamine, E. K. (1960). *Preventing the darkening of fresh lychees prepared for export* (Technical progress report No. 127). Hawaii Agricultural Experiment Station. University of Hawaii. https://scholarspace.manoa.hawaii.edu/server/api/core/bitstreams/d951fcd7-499c-467d-8ea8-6b75cd1a9a06/content

Akamine, E. K., & Goo, T. (1977). *Effects of gamma irradiation on shelf life of fresh lychees (Litchi chinensis Sonn.)* (Bulletin No. 169). Hawaii Agricultural Experiment Station. University of Hawaii.

Ali, S., Khan, A. S., & Malik, A. U. (2016). Postharvest L-cysteine application delayed pericarp browning, suppressed lipid peroxidation and maintained antioxidative activities of litchi fruit. *Postharvest Biology and Technology*, *121*, 135–142. https://doi.org/10.1016/j.postharvbio.2016.07.015

Ali, S., Khan, A. S., Malik, A. U., Anjum, M. A., Nawaz, A., & Shah, H. M. S. (2019). Modified atmosphere packaging delays enzymatic browning and maintains quality of harvested litchi fruit during low temperature storage. *Scientia Horticulturae*, *254*, 14–20. https://doi.org/10.1016/j.scienta.2019.04.065

Ali, S., Khan, A. S., Malik, A. U., Shaheen, T., & Shahid, M. (2018). Pre-storage methionine treatment inhibits postharvest enzymatic browning of cold stored 'Gola' litchi fruit. *Postharvest Biology and Technology*, *140*, 100–106. https://doi.org/10.1016/j.postharvbio.2018.02.016

Ali, S., Khan, A. S., Malik, A. U., & Shahid, M. (2016). Effect of controlled atmosphere storage on pericarp browning, bioactive compounds and antioxidant enzymes of litchi fruits. *Food Chemistry*, *206*, 18–29. https://doi.org/10.1016/j.foodchem.2016.03.021

Ali, S., Khan, A. S., Nawaz, A., Anjum, M. A., Naz, S., Ejaz, S., & Hussain, S. (2019). Aloe vera gel coating delays postharvest browning and maintains quality of harvested litchi fruit. *Postharvest Biology and Technology*, *157*, 110960. https://doi.org/10.1016/j.postharvbio.2019.110960

Anon. (2022). *Polyphenol oxidase*. https://en.wikipedia.org/wiki/Polyphenol_oxidase

Archibald, A. J., & Bower, J. P. (2008). Effect of temperature management and packaging on retention of litchi colour and quality. *Acta Horticulturae*, *768*, 225–232. https://doi.org/10.17660/ActaHortic.2008.768.27

Baldwin, I. T. (2010). Plant volatiles. *Current Biology*, *20*(9), R392–R397. https://doi.org/10.1016/j.cub.2010.02.052

Barman, K., Siddiqui, M. W., Patel, V. B., & Prasad, M. (2014). Nitric oxide reduces pericarp browning and preserves bioactive antioxidants in litchi. *Scientia Horticulturae*, *171*, 71–77. https://doi.org/10.1016/j.scienta.2014.03.036

Bouwmeester, H., Schuurink, R. C., Bleeker, P. M., & Schiestl, F. (2019). The role of volatiles in plant communication. *The Plant Journal*, *100*(5), 892–907. https://doi.org/10.1111/tpj.14496

Brand-Miller, J. C., Stockmann, K., Atkinson, F., Petocz, P., & Denyer, G. (2009). Glycemic index, postprandial glycemia, and the shape of the curve in healthy subjects: Analysis of a database of more than 1000 foods. *The American Journal of Clinical Nutrition*, *89*(1), 97–105. https://doi.org/10.3945/ajcn.2008.26354

Bryant, P. H. (2012). A model of postharvest moisture loss under air currents to reduce pericarp browning of litchi (*Litchi chinensis* Sonn.). *Postharvest Biology and Technology*, *73*, 8–13. https://doi.org/10.1016/j.postharvbio.2012.05.006

Cabral, T. A., de Morais Cardoso, L., & Pinheiro-Sant'Ana, H. M. (2014). Chemical composition, vitamins and minerals of a new cultivar of lychee (*Litchi chinensis* cv. Tailandes) grown in Brazil. *Fruits*, *69*(6), 425–434. https://doi.org/10.1051/fruits/2014031

Cai, Z. G., Zhang, Z. Q., Fang, R. Q., Gong, J. J., Jiang, Y. M., & Pang, X. Q. (2010). Purification and characterization of anthocyanin degradation enzyme from litchi fruit pericarp. *Acta Horticulturae*, *863*, 545–552. https://doi.org/10.17660/ActaHortic.2010.863.76

Campbell, C. W. (1959). Storage behavior of fresh Brewster and Bengal lychees. *Proceedings of the Florida State Horticultural Society*, *72*, 356–360. https://journals.flvc.org/fshs/issue/view/4684

Caro, Y., & Joas, J. (2005). Postharvest control of litchi pericarp browning (cv. Kwai Mi) by combined treatments of chitosan and organic acids: II. Effect of the initial water content of pericarp. *Postharvest Biology and Technology*, *38*(2), 137–144. https://doi.org/10.1016/j.postharvbio.2005.06.012

Cavaletto, C. G. (1980). Lychee. In S. Nagy & P. E. Shaw (Eds.), *Tropical and subtropical fruits: Composition, properties and uses* (pp. 469–478). The AVI Publishing Company.

Chan, H. T., Jr., & Kwok, S. C. (1974). Nonvolatile acids in lychee. *Journal of Food Science*, *39*(4), 792–793. https://doi.org/10.1111/j.1365-2621.1974.tb17981.x

Chan, H. T., Jr., Kwok, S. C., & Lee, C. W. (1975). Sugar composition and invertase activity in lychee. *Journal of Food Science*, *40*(4), 772–774. https://doi.org/10.1111/j.1365-2621.1975.tb00553.x

Chen, W. X., Wu, Z. X., Ji, Z. L., Su, M. X., & Chen, W. X. (2001). Postharvest research and handling of litchi in China—A review. *Acta Horticulturae*, *558*, 321–329. https://doi.org/10.17660/ActaHortic.2001.558.53

Chen, X., Wu, Q., Chen, Z., Li, T., Zhang, Z., Gao, H., Yun, Z., & Jiang, Y. (2019). Changes in pericarp metabolite profiling of four litchi cultivars during browning. *Food Research International*, *120*, 339–351. https://doi.org/10.1016/j.foodres.2019.02.046

Chen, Y. Y., Wu, P. C., Weng, S. F., & Liu, J. F. (2011). Glycemia and peak incremental indices of six popular fruits in Taiwan: Healthy and type 2 diabetes subjects compared. *Journal of Clinical Biochemistry and Nutrition*, *49*(3), 195–199. https://doi.org/10.3164/jcbn.11-11

Chu, C. G., Leung, S. E., & Kawaji, M. (2004). Reversibility of lychee pericarp red color in relation to pericarp pH, activity of polyphenol oxidase, and particle size of brown pigment. *Fruits*, *59*(1), 17–23. https://doi.org/10.1051/fruits:2004002

Chyau, C. C., Ko, P. T., Chang, C. H., & Mau, J. L. (2003). Free and glycosidically bound aroma compounds in lychee (*Litchi chinensis* Sonn.). *Food Chemistry*, *80*(3), 387–392. https://doi.org/10.1016/S0308-8146(02)00278-9

Clements, R. S., Jr., & Darnell, B. (1980). Myo-inositol content of common foods: Development of a high-myo-inositol diet. *The American Journal of Clinical Nutrition*, *33*(9), 1954–1967. https://doi.org/10.1093/ajcn/33.9.1954

Coates, L. M., Johnson, G. I., Sardsud, U., & Cooke, A. W. (1994). Postharvest diseases of lychee in Australia, and their control. In G. I. Johnson & E. Highley (Eds.), *Development of postharvest handling technology for tropical tree fruits* (pp. 68–69). Proceedings Australian Centre for International Agricultural Research (ACIAR). https://www.aciar.gov.au/publication/technical-publications/development-postharvest-handling-technology-tropical-tree-fruits

Cools, K., & Terry, L. A. (2012). Extraction and quantification of sugars and fructans from vegetable matter. In V. R. Preedy (Ed.), *Dietary sugars: Chemistry, analysis, function and effects* (pp. 249–268). The Royal Society of Chemistry. https://doi.org/10.1039/9781849734929-00249

Crowther, T., Collin, H. A., Smith, B., Tomsett, A. B., O'Connor, D., & Jones, M. G. (2005). Assessment of the flavour of fresh uncooked onions by taste-panels and analysis of flavour precursors, pyruvate and sugars. *Journal of the Science of Food and Agriculture*, *85*(1), 112–120. https://doi.org/10.1002/jsfa.1966

De Jager, E. S., & Korsten, L. (2003). Effect of fungicides and disinfectants in the prevention of litchi pericarp browning and control of postharvest diseases. *South African Litchi Growers' Association Yearbook*, *15*, 16–23.

De Jager, E. S., Wehner, F. C., & Korsten, L. (2003). Fungal postharvest pathogens of litchi fruit in South Africa. *South African Litchi Growers' Association Yearbook*, *15*, 24–32.

Deng, M., Deng, Y., Dong, L., Ma, Y., Liu, L., Huang, F., Wei, Z., Zhang, Y., Zhang, M., & Zhang, R. (2018). Effect of storage conditions on phenolic profiles and antioxidant activity of litchi pericarp. *Molecules*, *23*(9), 2276. https://doi.org/10.3390/molecules23092276

De Reuck, K., Sivakumar, D., & Korsten, L. (2009a). Effect of integrated application of chitosan coating and modified atmosphere packaging on overall quality retention in litchi cultivars. *Journal of the Science of Food and Agriculture*, *89*(5), 915–920. https://doi.org/10.1002/jsfa.3501

De Reuck, K., Sivakumar, D., & Korsten, L. (2009b). Integrated application of 1-methylcyclopropene and modified atmosphere packaging to improve quality retention of litchi cultivars during storage. *Postharvest Biology and Technology*, *52*(1), 71–77. https://doi.org/10.1016/j.postharvbio.2008.09.013

Dodd, M., Cronje, P., Taylor, M., Huysamer, M., Kruger, F., Lotz, E., & Van der Merwe, K. (2010). A review of the postharvest handling of fruits in South Africa over the past twenty-five years. *South African Journal of Plant and Soil*, *27*(1), 97–116. https://hdl.handle.net/10520/EJC87957

Duan, X., Jiang, Y., Su, X., Zhang, Z., & Shi, J. (2007). Antioxidant properties of anthocyanins extracted from litchi (*Litchi chinenesis* Sonn.) fruit pericarp tissues in relation to their role in the pericarp browning. *Food Chemistry*, *101*(4), 1365–1371. https://doi.org/10.1016/j.foodchem.2005.06.057

Duan, X., Liu, T., Zhang, D., Su, X., Lin, H., & Jiang, Y. (2011). Effect of pure oxygen atmosphere on antioxidant enzyme and antioxidant activity of harvested litchi fruit during storage. *Food Research International*, *44*(7), 1905–1911. https://doi.org/10.1016/j.foodres.2010.10.027

Ducamp-Collin, M. N. (2001). New litchi conservation techniques. *Fruitrop*, *85*, 22–23. (Abstract only). https://agritrop.cirad.fr/485186/1/ID485186.pdf

Ducamp-Collin, M. N., Ramarson, H., Lebrun, M., Self, G., & Reynes, M. (2008). Effect of citric acid and chitosan on maintaining red colouration of litchi fruit pericarp. *Postharvest Biology and Technology*, *49*(2), 241–246. https://doi.org/10.1016/j.postharvbio.2008.01.009

Duvenage, J. A., Mostert, M. M., & Marais, J. J. (1995). Postharvest sulphuring and low pH treatment for retention of red skin colour of litchi fruit. *South African Litchi Growers' Association Yearbook*, *7*, 44–46.

Duvenhage, J. A. (1993). Control of post-harvest decay and browning of litchi fruit by sodium metabisulphite and low pH dips. *South African Litchi Growers' Association Yearbook*, *5*, 31–32.

Fahima, A., Levinkron, S., Maytal, Y., Hugger, A., Lax, I., Huang, X., Eyal, Y., Lichter, A., Stern, R. A., & Harpaz-Saad, S. (2019). Cytokinin treatment modifies litchi fruit pericarp anatomy leading to reduced susceptibility to post-harvest pericarp browning. *Plant Science*, *283*, 41–50. https://doi.org/10.1016/j.plantsci.2019.02.006

Fang, F., Zhang, X. L., Luo, H. H., Zhou, J. J., Gong, Y. H., Li, W. J., Shi, Z. W., He, Q., Wu, Q., Lu, L., Jiang, L. L., Cai, Z. G., Oren-Shamir, M., Zhang, Z. Q., & Pang, X. Q. (2015). An intracellular laccase is responsible for epicatechin-mediated anthocyanin degradation in litchi fruit pericarp. *Plant Physiology*, *169*(4), 2391–2408. https://doi.org/10.1104/pp.15.00359

Fang, F., Zhang, Z. Q., Zhang, X. L., Wu, Z. X., Yin, H. F., & Pang, X. Q. (2013). Reduction in activity/gene expression of anthocyanin degradation enzymes in lychee pericarp is responsible for the color protection of the fruit by heat and acid treatment. *Journal of Integrative Agriculture*, *12*(9), 1694–1702. https://doi.org/10.1016/S2095-3119(13)60410-4

Fär, J., Wüthrich, B., & Vieths, S. (1995). Anaphylactic reaction to lychee fruit: Evidence for sensitization to profilin. *Clinical & Experimental Allergy*, *25*(10), 1018–1023. https://doi.org/10.1111/j.1365-2222.1995.tb00405.x

Farina, V., Gianguzzi, G., D'Asaro, A., Mazzaglia, A., & Palazzolo, E. (2017). Fruit production and quality evaluation of four litchi cultivars (*Litchi chinensis* Sonn.) grown in Mediterranean climate. *Fruits*, *72*(4), 203–211. https://doi.org/10.17660/th2017/72.4.2

FDA. (1986). *Food and Drug Administration food labelling: declaration of sulfiting agents*. Federal Register 51, 25012–25026.

Feng, S., Huang, M., Crane, J. H., & Wang, Y. (2018). Characterization of key aroma-active compounds in lychee (*Litchi chinensis* Sonn.). *Journal of Food and Drug Analysis*, *26*(2), 497–503. https://doi.org/10.1016/j.jfda.2017.07.013

Feng, S., Li, M. F., Wu, F., Li, W. L., & Li, S. P. (2015). 5-Aminolevulinic acid affects fruit coloration, growth, and nutrition quality of *Litchi chinensis* Sonn. cv. Feizixiao in Hainan, tropical China. *Scientia Horticulturae*, *193*, 188–194. https://doi.org/10.1016/j.scienta.2015.07.010

Follett, P. A. (2009). Generic radiation quarantine treatments: The next steps. *Journal of Economic Entomology*, *102*(4), 1399–1406. https://doi.org/10.1603/029.102.0401

Follett, P. A., & Neven, L. G. (2006). *Current trends in quarantine entomology*. https://digitalcommons.unl.edu/usdaarsfacpub/346/

Follett, P. A., & Sanxter, S. S. (2003). Lychee quality after hot-water immersion and X-ray irradiation quarantine treatments. *HortScience*, *38*(6), 1159–1162. https://doi.org/10.21273/HORTSCI.38.6.1159

Foster, A. C., & Kemp, J. A. (2006). Glutamate-and GABA-based CNS therapeutics. *Current Opinion in Pharmacology*, *6*(1), 7–17. https://doi.org/10.1016/j.coph.2005.11.005

Froehlich, O., & Schreier, P. (1986). Additional neutral volatiles from litchi (*Litchi chinensis* Sonn.) fruit. *Flavour and Fragrance Journal*, *1*(4–5), 149–153. https://doi.org/10.1002/ffj.2730010404

Fuchs, Y., Zauberman, G., Ronen, R., Rot, I., Weksler, A., & Akerman, M. (1993). The physiological basis of litchi fruit pericarp color retention. *Physiological Basis of Postharvest Technologies*, *343*, 29–33. https://doi.org/10.17660/ActaHortic.1993.343.6

Furuno, K., Akasako, T., & Sugihara, N. (2002). The contribution of the pyrogallol moiety to the superoxide radical scavenging activity of flavonoids. *Biological and Pharmaceutical Bulletin*, *25*(1), 19–23. https://doi.org/10.1248/bpb.25.19

Gao, Z., Hu, M., Zhao, C., Zhang, Z., Li, M., Li, H., Wang, G., Sun, J., Wen, J., & Wang, J. (2018). Effects of energy charge levels and expression of energy charge genes on browning of post-harvest litchi fruit.

Acta Horticulturae Sinica, *45*(1), 51–60. (In Chinese with English abstract). http://www.ahs.ac.cn/EN/abstract/abst

Gao, Z. Y., Zhao, C., Hu, M. J., Li, M., Li, H. L., Wang, G., Sun, J. H., & Wang, J. B. (2018). Effects of energy supply on energy metabolism and postharvest senescence of 'Nandao wuhe' litchi fruit. *Chinese Journal of Tropical Crops*, *39*, 254–259. (In Chinese with English abstract).

Gong, Q. Q., & Tian, S. P. (2002). Partial characterization of soluble peroxidase in pericarp of litchi fruit. *Sheng wu hua xue yu Sheng wu wu li jin Zhan*, *29*(6), 891–896.

Hatton, T. T., Reeder, W. F., & Kaufman, J. (1966). *Maintaining market quality of fresh lychees during storage and transit* (USDA Marketing Research Report No. 770). https://books.google.com/books?id=Zus8AAAAYAAJ&ots=23qYoG4mqk&;dq=Hatton%2C%20T.T.%2C%20Wm.F.%20Reeder%2C%20and%20J.%20Kaufman.%201966.%20Maintaining%20market%20quality%20of%20fresh%20lychees%20during%20storage%20and%20transit.%20USDA%20Marketing%20Research%20Report%20No.%20770%20p.1-9.%20&lr&pg=PA2#v=onepage&q&f=false

Haytowitz, D. B., Lemar, L. E., & Pehrsson, P. R. (2009). USDA's Nutrient Databank System—A tool for handling data from diverse sources. *Journal of Food Composition and Analysis*, *22*(5), 433–441. https://doi.org/10.1016/j.jfca.2009.01.003

Higgins, J. E. (1917). *The litchi in Hawaii* (Bulletin No. 44). Hawaiian Agriculture Experiment Station. http://hdl.handle.net/10125/9172

Holcroft, D. M., Lin, H., & Ketsa, S. (2005). Harvesting and storage. In C. Menzel & G. K. Waite (Eds.), *Litchi and longan: Botany, production and uses* (pp. 273–295). CAB International United Kingdom. https://doi.org/10.1079/9780851996967.0000

Holcroft, D. M., & Mitcham, E. J. (1996). Postharvest physiology and handling of litchi (*Litchi chinensis* Sonn.). *Postharvest Biology and Technology*, *9*(3), 265–281. https://doi.org/10.1016/S0925-5214(96)00037-3

Hoppe, S., Neidhart, S., Zunker, K., Hutasingh, P., Carle, R., Steinhart, H., & Paschke, A. (2006). The influences of cultivar and thermal processing on the allergenic potency of lychees (*Litchi chinensis* SONN.). *Food Chemistry*, *96*(2), 209–219. https://doi.org/10.1016/j.foodchem.2005.02.020

Hoppe, S., Steinhart, H., & Paschke, A. (2006). Identification of a 28 kDa lychee allergen as a triose-phosphate isomerase. *Food and Agricultural Immunology*, *17*(1), 9–19. https://doi.org/10.1080/09540100500538307

Hu, B., Li, J., Wang, D., Wang, H., Qin, Y., Hu, G., & Zhao, J. (2018). Transcriptome profiling of *Litchi chinensis* pericarp in response to exogenous cytokinins and abscisic acid. *Plant Growth Regulation*, *84*(3), 437–450. https://doi.org/10.1007/s10725-017-0351-7

Hu, W. R., Ji, Z. L., Liu, S. Z., & Zhang, Z. Q. (2004a). Changes of pericarp color and the content of anthocyanin and flavonoids in litchi pericarp during chilling-injured temperature storage. *Acta Horticulturae Sinica*, *31*, 723–726. (In Chinese with English abstract) https://www.ahs.ac.cn/EN/Y2004/V31/I6/723

Hu, W. R., Liu, S. Z., Pang, X. Q., Ji, Z. L., & Zhang, Z. Q. (2010). Alleviation of chilling injury in litchi fruit by ABA application. *Acta Horticulturae*, *863*, 533–538. https://doi.org/10.17660/ActaHortic.2010.863.74

Hu, W. R., Liu, S. Z., Zhang, Z. Q., & Ji, Z. L. (2005). Changes of lipoxygenase activity of postharvest litchi fruit. *Journal of Huazhong Agricultural University (Huazhong Nongye Daxue Xuebao)*, *24*, 285–289. (In Chinese with English abstract).

Hu, W. R., Liu, S. Z., Zhang, Z. Q., Jiang, Y. M., & Ji, Z. L. (2006a). Changes of polyamines contents during chilling injury of litchi fruit. *Guangxi Plants*, *26*, 370–374. (In Chinese with English abstract).

Hu, W. R., Liu, S. Z., Zhang, Z. Q., Jiang, Y. M., & Ji, Z. L. (2006b). Reduction of chilling injury in litchi fruit by 1-MCP. *Acta Horticulturae Sinica*, *33*(6), 1203. (In Chinese with English abstract). https://www.ahs.ac.cn/EN/Y2006/V33/I6/1203

Hu, W. R., Pang, X. Q., Liu, S. Z., Zhang, Z. Q., & Ji, Z. L. (2005). Effects of postharvest handling on the anthocyanin content and anthocyanase activity in litchi pericarp. *Journal of Fruit Science*, *22*, 224–228. (In Chinese with English abstract).

Hu, W. R., Zhang, Z. Q., Ji, Z. L., & Liu, S. Z. (2004c). Study on acid treatment effects on pericarp color and physiological characteristics of litchi fruit. *Food Science*, *25*, 176–180. (In Chinese with English abstract).

Hu, W. R., Zhang, Z. Q., Ji, Z. L. L., & Liu, S. Z. (2004b). Effect of chilling injury on membrane lipid peroxidation and activities of cell defense enzyme in litchi pericarp. *Hua nan Nong ye da xue xue bao (Journal of South China Agricultural University)*, *25*(3), 6–9. (In Chinese with English abstract). https://europepmc.org/article/cba/571161

Hu, Z. Q., Huang, X. M., Chen, H. B., & Wang, H. C. (2010). Antioxidant capacity and phenolic compounds in litchi (*Litchi chinensis* Sonn.) pericarp. *Acta Horticulturae*, *86*, 567–574. https://doi.org/10.17660/ActaHortic.2010.863.79

Huang, C. C., Wang, Y. T., & Pan, C. H. (1991). Effect of storage temperature on the color and quality of litchi fruit. *Journal of the Chinese Society of Horticultural Science*, *37*, 141–152. (In Chinese with English abstract).

Huang, H. B., & Qiu, Y. X. (1987). Growth correlations and assimilate partitioning in the arillate fruit of *Litchi chinensis* Sonn. *Functional Plant Biology*, *14*(2), 181–188. https://doi.org/10.1071/PP9870181

Huang, H. B., & Xu, J. A. (1983). The developmental patterns of fruit tissues and their correlative relationships in *Litchi chinensis* Sonn. *Scientia Horticulturae*, *19*, 335–342. https://doi.org/10.1016/0304-4238(83)90081-X

Huang, S., Hart, H., Lee, H., & Wicker, L. (1990). Enzymatic and color changes during post-harvest storage of lychee fruit. *Journal of Food Science*, *55*(6), 1762–1763. https://doi.org/10.1111/j.1365-2621.1990.tb03623.x

Huang, X. M., Wang, H. C., Gao, F. F., & Huang, H. B. (1999). A comparative study of the pericarp of litchi cultivars susceptible and resistant to fruit cracking. *The Journal of Horticultural Science and Biotechnology*, *74*(3), 351–354. https://doi.org/10.1080/14620316.1999.11511120

Huang, X. M., Wang, H. C., Yuan, W. Q., Lu, J. M., Yin, J. H., Luo, S., & Huang, H. B. (2005). A study of rapid senescence of detached litchi: Roles of water loss and calcium. *Postharvest Biology and Technology*, *36*(2), 177–189. https://doi.org/10.1016/j.postharvbio.2004.12.005

Huang, X. M., Yuan, W. Q., Wang, H. C., Li, J. G., Huang, H. B., Shi, L., & Jinhua, Y. (2004). Linking cracking resistance and fruit desiccation rate to pericarp structure in litchi (*Litchi chinensis* Sonn.). *The Journal of Horticultural Science and Biotechnology*, *79*(6), 897–905. https://doi.org/10.1080/14620316.2004.11511863

Huang, X. Y., Kang, D. M., & Ji, Z. L. (1990). The optimum storage temperature for litchi fruits and chilling injury to them. *Journal of the South China Agricultural University*, *11*(3), 13–18. (In Chinese with English abstract). https://xuebao.scau.edu.cn/zr/hnny_zren/article/abstract/19900338?st=article_issue

Jacobi, K. K., Wong, L. S., & Giles, J. E. (1993). Lychee (*Litchi chinensis* Sonn.) fruit quality following vapour heat treatment and cool storage. *Postharvest Biology and Technology*, *3*(2), 111–119. https://doi.org/10.1016/0925-5214(93)90003-L

Jacobs, R., & Korsten, L. (2004). Preliminary identification of *Penicillium* species isolated through the litchi export chain from South Africa to distribution centers in the Netherlands and United Kingdom. *South African Litchi Growers' Association Yearbook*, *16*, 34–39.

Jiang, G., Xiao, L., Yan, H., Zhang, D., Wu, F., Liu, X. C., Su, X. G., Dong, X. H., Wang, J. H., Duan, X. W., & Jiang, Y. (2017). Redox regulation of methionine in calmodulin affects the activity levels of senescence-related transcription factors in litchi. *Biochimica et Biophysica Acta -General Subjects*, *1861*(5), 1140–1151. https://doi.org/10.1016/j.bbagen.2017.02.004

Jiang, J., Su, M., & Lee, P. (1986). The production and physiological effects of ethylene during ontogeny and after harvest of Litchi fruit. *Acta Phytophysiologia Sinica*, *12*, 95–103. (In Chinese with English abstract).

Jiang, X., Lin, H., Shi, J., Neethirajan, S., Lin, Y., Chen, Y., Wang, H., & Lin, Y. (2018). Effects of a novel chitosan formulation treatment on quality attributes and storage behavior of harvested litchi fruit. *Food Chemistry*, *252*, 134–141. https://doi.org/10.1016/j.foodchem.2018.01.095

Jiang, Y. (2000). Role of anthocyanins, polyphenol oxidase and phenols in lychee pericarp browning. *Journal of the Science of Food and Agriculture*, *80*(3), 305–310. https://doi.org/10.1002/1097-0010(200002)80:3%3C305::AID-JSFA518%3E3.0.CO;2-H

Jiang, Y., Duan, X., Joyce, D., Zhang, Z., & Li, J. (2004). Advances in understanding of enzymatic browning in harvested litchi fruit. *Food Chemistry*, *88*(3), 443–446. https://doi.org/10.1016/j.foodchem.2004.02.004

Jiang, Y., & Fu, J. (1998). Inhibition of polyphenol oxidase and the browning control of litchi fruit by glutathione and citric acid. *Food Chemistry*, *62*(1), 49–52. https://doi.org/10.1016/S0308-8146(97)00144-1

Jiang, Y., Fu, J., Zauberman, G., & Fuchs, Y. (1999). Purification of polyphenol oxidase and the browning control of litchi fruit by glutathione and citric acid. *Journal of the Science of Food and Agriculture*, *79*(7), 950–954. https://doi.org/10.1002/(SICI)1097-0010(19990515)79:7%3C950::AID-JSFA289%3E3.0.CO;2-E

Jiang, Y., Li, Y., & Li, J. (2004). Browning control, shelf life extension and quality maintenance of frozen litchi fruit by hydrochloric acid. *Journal of Food Engineering*, *63*(2), 147–151. https://doi.org/10.1016/S0260-8774(03)00293-0

Jiang, Y., Yao, L., Lichter, A., & Li, J. (2003). Postharvest biology and technology of litchi fruit. *International Journal of Food, Agriculture & Environment*, *1*, 76–81.

Jiang, Y. M. (2001). Properties of litchi polyphenol oxidase. *Acta Horticulturae*, *558*, 367–373. https://doi.org/10.17660/ActaHortic.2001.558.59

Jiang, Y. M., & Chen, F. (1995). A study on polyamine change and browning of fruit during cold storage of litchi (*Litchi chinensis* Sonn.). *Postharvest Biology and Technology*, *5*(3), 245–250. https://doi.org/10.1016/0925-5214(94)00021-J

Jiang, Y. M., & Fu, J. R. (1999a). Biochemical and physiological changes involved in browning of litchi fruit caused by water loss. *The Journal of Horticultural Science and Biotechnology*, *74*(1), 43–46. https://doi.org/10.1080/14620316.1999.11511069

Jiang, Y. M., & Fu, J. R. (1999b). Postharvest browning of litchi fruit by water loss and its prevention by controlled atmosphere storage at high relative humidity. *LWT—Food Science and Technology*, *32*(5), 278–283. https://doi.org/10.1006/fstl.1999.0546

Jiang, Y. M., Wang, Y., Song, L., Liu, H., Lichter, A., Kerdchoechuen, O., Joyce, D. C., & Shi, J. (2006). Postharvest characteristics and handling of litchi fruit—An overview. *Australian Journal of Experimental Agriculture*, *46*(12), 1541–1556. https://doi.org/10.1071/EA05108

Jiang, Y. M., Zauberman, G., & Fuchs, Y. (1997). Partial purification and some properties of polyphenol oxidase extracted from litchi fruit pericarp. *Postharvest Biology and Technology*, *10*(3), 221–228. https://doi.org/10.1016/S0925-5214(96)01404-4

Jing, G., Huang, H., Yang, B., Li, J., Zheng, X., & Jiang, Y. (2013). Effect of pyrogallol on the physiology and biochemistry of litchi fruit during storage. *Chemistry Central Journal*, *7*(1), 1–11. https://doi.org/10.1186/1752-153X-7-19

Joas, J., Caro, Y., Ducamp, M. N., & Reynes, M. (2005). Postharvest control of pericarp browning of litchi fruit (*Litchi chinensis* Sonn cv Kwaï Mi) by treatment with chitosan and organic acids: I. Effect of pH and pericarp dehydration. *Postharvest Biology and Technology*, *38*(2), 128–136. https://doi.org/10.1016/j.postharvbio.2005.06.013

Johnston, J. C., Welch, R. C., & Hunter, G. L. K. (1980). Volatile constituents of litchi (*Litchi chinesis* Sonn.). *Journal of Agricultural and Food Chemistry*, *28*(4), 859–861. https://doi.org/10.1021/jf60230a021

Joubert, A. (1986). Litchi. In S. P. Monselise (Ed.), *Handbook of fruit set and development* (pp. 233–246). CRC Press.

Jurd, L. (1964). Reactions involved in sulfite bleaching of anthocyanins. *Journal of Food Science*, *29*(1), 16–19. https://doi.org/10.1111/j.1365-2621.1964.tb01685.x

Kader, A. A. (1998). *Lychee—Recommendations for maintaining postharvest quality*. https://postharvest.ucdavis.edu/Commodity_Resources/Fact_Sheets/Datastores/Fruit_English/?uid=35&ds=798

Ketsa, S., & Leelawatana, K. (1992a). Effect of pre and post storage acid dipping on browning of lychee fruits. *Acta Horticulturae*, *321*, 726–731. https://doi.org/10.17660/ActaHortic.1992.321.91

Ketsa, S., & Leelawatana, K. (1992b). Effect of precooling and polyethylene film liners in corrugated boxes on quality of lychee fruits. *Acta Horticulturae*, *321*, 742–746. https://doi.org/10.17660/ActaHortic.1992.321.93

Koul, B., & Taak, P. (2017). Lychee (*Litchi chinensis* Sonn.): Pre-and post-harvest disease management. *Lychee disease management* (pp. 1–26). Springer. https://doi.org/10.1007/978-981-10-4247-8_1

Kramchote, S., Wongs-Aree, C., Srilaong, V., Uthairatanakij, A., & Kanlayanarat, S. (2008). Influence of nitric oxide on pericap browning of litchi cv. 'Chakrapad'. *Acta Horticulturae*, *804*, 249–254. https://doi.org/10.17660/ActaHortic.2008.804.33

Kramer, M. S., & Kuhn, G. D. (1964). The effect of radiation on mold populations on fresh lychees. *Proceedings of the Florida State Horticultural Society*, *77*, 436–438. https://journals.flvc.org/fshs/issue/view/4684

Kremer-Köhne, S. (1993). SO_2 residues in litchi fruit after post-harvest SO_2 treatments (1990). *South African Litchi Growers' Association Yearbook*, *5*, 15–16.

Kumar, D., Mishra, D. S., Chakraborty, B., & Kumar, P. (2013). Pericarp browning and quality management of litchi fruit by antioxidants and salicylic acid during ambient storage. *Journal of Food Science and Technology*, *50*(4), 797–802. https://doi.org/10.1007/s13197-011-0384-2

Kumari, P., Barman, K., Patel, V. B., Siddiqui, M. W., & Kole, B. (2015). Reducing postharvest pericarp browning and preserving health promoting compounds of litchi fruit by combination treatment of salicylic acid and chitosan. *Scientia Horticulturae*, *197*, 555–563. https://doi.org/10.1016/j.scienta.2015.10.017

Lai, B., Du, L. N., Hu, B., Wang, D., Huang, X. M., Zhao, J. T., Wang, H. C., & Hu, G. B. (2019). Characterization of a novel litchi R2R3-MYB transcription factor that involves in anthocyanin biosynthesis and tissue acidification. *BMC Plant Biology*, *19*(1), 1–13. https://doi.org/10.1186/s12870-019-1658-5

Lai, B., Du, L. N., Liu, R., Hu, B., Su, W. B., Qin, Y. H., Zhao, J. T., Wang, H. C., & Hu, G. B. (2016). Two LcbHLH transcription factors interacting with LcMYB1 in regulating late structural genes of anthocyanin biosynthesis in Nicotiana and Litchi chinensis during anthocyanin accumulation. *Frontiers in Plant Science*, *7*, 166. https://doi.org/10.3389/fpls.2016.00166

Lai, B., Hu, B., Qin, Y. H., Zhao, J. T., Wang, H. C., & Hu, G. B. (2015). Transcriptomic analysis of *Litchi chinensis* pericarp during maturation with a focus on chlorophyll degradation and flavonoid biosynthesis. *BMC Genomics*, *16*(1), 1–18. https://doi.org/10.1186/s12864-015-1433-4

Lai, B., Li, X. J., Hu, B., Qin, Y. H., Huang, X. M., Wang, H. C., & Hu, G. B. (2014). LcMYB1 is a key determinant of differential anthocyanin accumulation among genotypes, tissues, developmental phases and ABA and light stimuli in *Litchi chinensis*. *PLoS One*, *9*(1), e86293. https://doi.org/10.1371/journal.pone.0086293

Lai, D., Shao, X., Xiao, W., Fan, C., Liu, C., He, H., Tian, S. Y., & Kuang, S. (2020). Suppression of fruit decay and maintenance of storage quality of litchi by *Photorhabdus luminescens* Hb1029 treatment. *Scientia Horticulturae*, *259*, 108836. https://doi.org/10.1016/j.scienta.2019.108836

Lee, H. S., & Wicker, L. (1991a). Anthocyanin pigments in the skin of lychee fruit. *Journal of Food Science*, *56*(2), 466–468. https://doi.org/10.1111/j.1365-2621.1991.tb05305.x

Lee, H. S., & Wicker, L. (1991b). Quantitative changes in anthocyanin pigments of lychee fruit during refrigerated storage. *Food Chemistry*, *40*(3), 263–270. https://doi.org/10.1016/0308-8146(91)90111-Z

Lemmer, D., & Kruger, F. J. (2000a). Factors influencing SO_2 residues on commercially fumigated 'HLH Mauritius' and 'McLean's Red' litchi fruit. *South African Litchi Growers' Association Yearbook*, *11*, 42–46.

Lemmer, D., & Kruger, F. J. (2000b). Research on alternative postharvest treatments for litchi fruit. *South African Litchi Growers' Association Yearbook*, *11*, 37–39.

Lemmer, D., Kruger, F. J., & Kruger, C. (2001). Development and refinement of litchi postharvest treatments. *South African Litchi Growers' Association Yearbook*, *12*, 25–30.

Li, M. F., Feng, S., Li, S. P., Wu, F., Wang, F., Li, C. L., Fu, Y. N., Bao, D. H., & Wang, L. J. (2019). Preharvest promotion or inhibition of colouration: Which is the more conducive to improving litchi postharvest quality? *Scientia Horticulturae*, *254*, 124–132. https://doi.org/10.1016/j.scienta.2019.04.083

Li, T., He, M., Zeng, J., Chen, Z., Hongxia, Q., Duan, X., & Jiang, Y. (2020). Choline chloride alleviates the pericarp browning of harvested litchi fruit by inhibiting energy deficiency mediated programmed cell death. *Postharvest Biology and Technology*, *167*, 111224. https://doi.org/10.1016/j.postharvbio.2020.111224

Li, T., Shi, D., Wu, Q., Zhang, Z., Qu, H., & Jiang, Y. (2019). Sodium para-aminosalicylate delays pericarp browning of litchi fruit by inhibiting ROS-mediated senescence during postharvest storage. *Food Chemistry*, *278*, 552–559. https://doi.org/10.1016/j.foodchem.2018.11.099

Li, T., Zhu, H., Wu, Q., Yang, C., Duan, X., Qu, H., Yun, Z., & Jiang, Y. (2015). Comparative proteomic approaches to analysis of litchi pulp senescence after harvest. *Food Research International*, *78*, 274–285. https://doi.org/10.1016/j.foodres.2015.09.033

Li, X., Chen, W., & Liu, A. (2006). Effects of *Colletotrichum gloeosporioides* infection on physiological and biochemical changes of litchi fruit. *Subtropical Plant Science*, *35*, 1–4. http://www.yrdzwkx.com/EN/abstract/abstract1436.shtml

Li, X., Liu, A., & Chen, W. (2005). Studies on development and control of anthracnose of lychee fruit before and after harvest. *Acta Horticulturae*, *665*, 409–413. https://doi.org/10.17660/ActaHortic.2005.665.51

Liang, Y. S., Chen, N. L., & Ke, L. S. (2012). Influence of dipping in sodium metabisulfite on pericarp browning of litchi cv. Yu Her Pau (Feizixiao). *Postharvest Biology and Technology*, *68*, 72–77. https://doi.org/10.1016/j.postharvbio.2012.02.005

Lichter, A., Dvir, O., Ackerman, M., Feygenberg, O., & Pesis, E. (2004). Acidified peel of litchi fruits selects for postharvest Penicillium decay. *Phytoparasitica*, *32*(3), 226–236. https://doi.org/10.1007/BF02979817

Lichter, A., Dvir, O., Rot, I., Akerman, M., Regev, R., Wiesblum, A., Fallik, E., Zauberman, G., & Fuchs, Y. (2000). Hot water brushing: An alternative method to SO_2 fumigation for color retention of litchi fruits. *Postharvest Biology and Technology*, *18*(3), 235–244. https://doi.org/10.1016/S0925-5214(99)00077-0

Lichter, A., Zutahy, Y., Kaplunov, T., & Lurie, S. (2008). Evaluation of table grape storage in boxes with sulfur dioxide-releasing pads with either an internal plastic liner or external wrap. *HortTechnology*, *18*(2), 206–214. https://doi.org/10.21273/HORTTECH.18.2.206

Lin, B., Du, Y., Liang, X., Wang, X., Wang, X., & Yang, J. (2011). Effect of chitosan coating on respiratory behavior and quality of stored litchi under ambient temperature. *Journal of Food Engineering*, *102*(1), 94–99. https://doi.org/10.1016/j.jfoodeng.2010.08.009

Lin, Z. F., Li, S. S., Lin, C. D., Lin, G. D., Li, Y. B., Liu, S. X., & Chen, M. D. (1988). The changes of pigments, phenolics contents and activities of polyphenol oxidase and phenylalanine ammonia-lyase in pericarp of postharvest litchi fruit. *Journal of Integrative Plant Biology (Acta Botanica Sinica)*, *30*, 40–45. (In Chinese with English abstract). https://www.jipb.net/EN/abstract/abstract27085.shtml

Lin, Z. F., Li, S. S., Zhang, D. L., Liu, S. X., Li, Y. B., Lin, G. Z., & Chen, M. D. (1988). The changes of oxidation and peroxidation in postharvest litchi fruit. *Journal of Integrative Plant Biology (Acta Botanica Sinica)*, *30*, 382–387. (In Chinese with English abstract). https://www.jipb.net/EN/abstract/abstract27011.shtml

Liu, A., Chen, W., & Li, X. (2005). Changes in the postharvest physiology and lychee fruits latently infected by anthracnose fungus and the biological characteristic of the pathogenic fungus of the disease. *Acta Horticulturae*, *665*, 365–372. https://doi.org/10.17660/ActaHortic.2005.665.45

Liu, A., Chen, W., & Li, X. (2006). Developments of anthracnose on harvested litchi fruits and the effects of the disease on storage of the fruits. *Acta Phytophylacica Sinica*, *33*, 351–356. (In Chinese with English abstract).

Liu, G., Zhang, Y., Yun, Z., Hu, M., Liu, J., Jiang, Y., & Zhang, Z. (2020). Melatonin enhances cold tolerance by regulating energy and proline

metabolism in litchi fruit. *Foods*, *9*(4), 454. https://doi.org/10.3390/foods9040454

Liu, H., Song, L., You, Y., Li, Y., Duan, X., Jiang, Y., Joyce, D. C., Ashraf, M., & Lu, W. (2011). Cold storage duration affects litchi fruit quality, membrane permeability, enzyme activities and energy charge during shelf time at ambient temperature. *Postharvest Biology and Technology*, *60*(1), 24–30. https://doi.org/10.1016/j.postharvbio.2010.11.008

Liu, J., Liu, A., & Chen, W. (2006). Effects of *Peronophythora litchi* infection on physiological changes of litchi fruit. *Southwest Horticulture*, *34*, 1–4. (In Chinese with English abstract).

Liu, L., Cao, S., Xu, Y., Zhang, M., Xiao, G., Deng, Q., & Xie, B. (2010). Oxidation of (−)-epicatechin is a precursor of litchi pericarp enzymatic browning. *Food Chemistry*, *118*(3), 508–511. https://doi.org/10.1016/j.foodchem.2009.05.019

Liu, R., Lai, B., Hu, B., Qin, Y., Hu, G., & Zhao, J. (2017). Identification of microRNAs and their target genes related to the accumulation of anthocyanins in Litchi chinensis by high-throughput sequencing and degradome analysis. *Frontiers in Plant Science*, *7*, 2059. https://doi.org/10.3389/fpls.2016.02059

Lonsdale, J. H., & Kremer-Köhne, S. (1990). Maintaining market quality of fresh litchis during storage. Part 2: Control of post-harvest decay. *South African Litchi Growers' Association Yearbook*, *3*, 18–20.

Luo, T., Li, S., Han, D., Guo, X., Shuai, L., & Wu, Z. (2019). The effect of desulfurization on the postharvest quality and sulfite metabolism in pulp of sulfitated "Feizixiao" Litchi (*Litchi chinensis* Sonn.) fruits. *Food Science & Nutrition*, *7*(5), 1715–1726. https://doi.org/10.1002/fsn3.1008

Luximon-Ramma, A., Bahorun, T., & Crozier, A. (2003). Antioxidant actions and phenolic and vitamin C contents of common Mauritian exotic fruits. *Journal of the Science of Food and Agriculture*, *83*(5), 496–502. https://doi.org/10.1002/jsfa.1365

Magwaza, L. S., & Opara, U. L. (2015). Analytical methods for determination of sugars and sweetness of horticultural products—A review. *Scientia Horticulturae*, *184*, 179–192. https://doi.org/10.1016/j.scienta.2015.01.001

Mangaraj, S., Goswami, T. K., & Mahajan, P. V. (2009). Applications of plastic films for modified atmosphere packaging of fruits and vegetables: A review. *Food Engineering Reviews*, *1*(2), 133–158. https://doi.org/10.1007/s12393-009-9007-3

Martínez-Bolaños, M., Téliz-Ortiz, D., Mora-Aguilera, A., Valdovinos-Ponce, G., Nieto-Ángel, D., García-Pérez, E., & Sánchez-López, V. (2015). Anthracnose (*Colletotrichum gloeosporioides Penz.*) of litchi fruit (*Litchi chinensis* Soon.) in *Oaxaca, Mexico*. *Revista Mexicana de Fitopatología*, *33*(2), 140–155. https://rmf.smf.org.mx/Vol_33_2_2015.html<./bib>

Martínez-Castellanos, G., Pelayo-Zaldívar, C., Pérez-Flores, L. J., López-Luna, A., Gimeno, M., Bárzana, E., & Shirai, K. (2011). Postharvest litchi (*Litchi chinensis* Sonn.) quality preservation by *Lactobacillus plantarum*. *Postharvest Biology and Technology*, *59*(2), 172–178. https://doi.org/10.1016/j.postharvbio.2010.09.005

McGuire, R. G. (1997). Response of lychee fruit to cold and gamma irradiation treatments for quarantine eradication of exotic pests. *HortScience*, *32*(7), 1255–1257. https://doi.org/10.21273/HORTSCI.32.7.1255

McGuire, R. G., & Baldwin, E. A. (1998). Acidic fruit coatings for maintenance of color and decay prevention on lychees postharvest. *Proceedings Florida State Horticultural Society*, *111*, 243–246. https://journals.flvc.org/fshs/issue/view/4174

Menzel, C. M., & Waite, G. K. (2005). *Litchi and longan: Botany, production and uses*. CABI Publishing. https://doi.org/10.1079/9780851996967.0000

Mhlophea, S. D., & Kruger, F. J. (2014). Evaluation of hydro-cooling as a postharvest treatment for sulphur dioxide fumigated 'Mauritius' litchi fruit. *Acta Horticulturae*, *1029*, 331–336. https://doi.org/10.17660/ActaHortic.2014.1029.41

Mitchell, G. E., McLauchlan, R. L., Isaacs, A. R., Williams, D. J., & Nottingham, S. M. (1992). Effect of low dose irradiation on composition of tropical fruits and vegetables. *Journal of Food Composition and Analysis*, *5*(4), 291–311. https://doi.org/10.1016/0889-1575(92)90063-P

Mitra, S. K. (2002). *Overview of lychee production in the Asia-Pacific region*. Lychee Production in the Asia Pacific Region. Food and Agricultural Organization of the United Nations. http://www.fao.org/3/ac684e/ac684e04.htm

Mizobutsi, G. P., Finger, F. L., Ribeiro, R. A., Puschmann, R., Neves, L. L. D. M., & Mota, W. F. D. (2010). Effect of pH and temperature on peroxidase and polyphenoloxidase activities of litchi pericarp. *Scientia Agricola*, *67*, 213–217. https://doi.org/10.1590/S0103-90162010000200013

Mizobutsi, G. P., Finger, F. L., Ribeiro, R. A., Puschmann, R., Vieira, G., & de Melo Neves, L. L. (2010). Influence of pH and temperature on polyphenoloxidase activity of lichi pericarp. *Acta Horticulturae*, *864*, 361–366. https://doi.org/10.17660/ActaHortic.2010.864.49

Nacif, S. R., Paoli, A. A. S., & Salomão, L. C. C. (2001). Morphological and anatomical development of the litchi fruit (*Litchi chinensis* Sonn. cv. Brewster). *Fruits*, *56*(4), 225–233. https://doi.org/10.1051/fruits:2001125

Nelson, K. E., & Ahmedullah, M. (1976). Packaging and decay-control systems for storage and transit of table grapes for export. *American Journal of Enology and Viticulture*, *27*(2), 74–79. https://doi.org/10.5344/ajev.1976.27.2.74

Neog, M., & Saikia, L. (2010). Control of post-harvest pericarp browning of litchi (*Litchi chinensis* Sonn). *Journal of Food Science and Technology*, *47*(1), 100–104. https://doi.org/10.1007/s13197-010-0001-9

Niggemann, B., Reibel, S., Hipler, C., & Wahn, U. (2002). Anaphylactic reaction to lychee in a 12-year-old girl: Cross-reactivity to latex? *Pediatric Allergy and Immunology*, *13*(1), 64–67. https://doi.org/10.1034/j.1399-3038.2002.00032.x

Nokthai, P., Lee, V. S., & Shank, L. (2010). Molecular modeling of peroxidase and polyphenol oxidase: Substrate specificity and active site comparison. *International Journal of Molecular Sciences*, *11*(9), 3266–3276. https://doi.org/10.3390/ijms11093266

Olesen, T., Nacey, L., Wiltshire, N., & O'Brien, S. (2004). Hot water treatments for the control of rots on harvested litchi (*Litchi chinensis* Sonn.) fruit. *Postharvest Biology and Technology*, *32*(2), 135–146. https://doi.org/10.1016/j.postharvbio.2003.10.009

Olesen, T., Wiltshire, N., & McConchie, C. (2003). *Effects of storage temperature and cooling methods on the storage life of lychee (Litchi chinensis Sonn.) fruit*. Rural Industries Research and Development Corporation. https://www.agrifutures.com.au/wp-content/uploads/publications/03-111.pdf

Ong, P. K. C., & Acree, T. E. (1998). Gas chromatography/olfactory analysis of lychee (*Litchi chinensis* Sonn.). *Journal of Agricultural and Food Chemistry*, *46*, 2282–2286. https://doi.org/10.1021/jf9801318

Oosthuyse, S. A. (2014). Effect of coating sulphured 'Madras' litchi fruits with PolymerCoat directly after harvest on the incidence of

Penicillium colonization after cold Storage. *Acta Horticulturae*, *1029*, 353–358. https://doi.org/10.17660/ActaHortic.2014.1029.44

Pandey, N., Joshi, S. K., Singh, C. P., Kumar, S., Rajput, S., & Khandal, R. K. (2013). Enhancing shelf life of litchi (*Litchi chinensis*) fruit through integrated approach of surface coating and gamma irradiation. *Radiation Physics and Chemistry*, *85*, 197–203. https://doi.org/10.1016/j.radphyschem.2012.11.003

Pang, X. Q., Huang, X. M., Yang, X. T., Ji, Z. L., & Zhang, Z. Q. (2008). Role of polyphenol oxidase in anthocyanin degradation of lychee pericarp. *Scientia Agricultura Sinica*, *41*, 540–545. (In Chinese with English abstract).

Pang, X. Q., Zhang, Z. Q., Duan, X. W., & Ji, Z. L. (2001a). Influence of pH and active oxygen on the stability of anthocyanins from litchi pericarp. *Acta Horticulturae*, *558*, 339–342. https://doi.org/10.17660/ActaHortic.2001.558.55

Pang, X. Q., Zhang, Z. Q., Duan, X. W., & Ji, Z. L. (2001b). Influence of pH and temperature on the stability of anthocyanin from litchi pericarp. *Acta Horticulturae Sinica*, *28*, 25–30. (In Chinese with English abstract).

Pang, X. Q., Zhang, Z. Q., Duan, X. W., & Ji, Z. L. (2001c). The effects of ethylene and 1-methylcyclopropene on pericarp browning of postharvest lychee fruit. *Journal of the South China Agricultural University*, *22*(4), 11–14. (In Chinese with English abstract). https://doi.org/10.7671/j.issn.1001-411X.2001.04.004

Pang, X. Q., Zhang, Z. Q., Duan, X. W., & Ji, Z. L. (2001d). The influence of oxidizing and reducing agents on the stability of anthocyanin in pericarp of lychee fruits. *Journal of the South China Agricultural University*, *22*(2), 15–17. (In Chinese with English abstract). http://doi.org/10.7671/j.issn.1001-411X.2001.02.005

Pareek, S. (2018). Nutritional and biochemical composition of lychee (*Litchi chinensis* Sonn.) Cultivars. In M. S. J. Simmonds & V. R. Preedy (Eds.), *Nutritional composition of fruit cultivars* (pp. 395–418). Elsevier. https://doi.org/10.1016/B978-0-12-408117-8.00017-9

Paull, R. E., Chen, C. C., & Chen, N. J. (2002). Litchi. In K. C. Gross, C. Y. Wang, & M. Saltveit (Eds.), *The commercial storage of fruits, vegetables, and florist and nursery crops* (pp. 3). United States Department of Agriculture. http://www.ba.ars.usda.gov/hb66/085litchi.pdf

Paull, R. E., Chen, C. C., & Chen, N. J. (2014). *Lychee: Postharvest quality-maintenance guidelines*. University of Hawaii at Manoa, College of Tropical Agriculture and Human Resources. Fruit, Nut, and Beverage Crops May 2014 F_N-29. http://www.ctahr.hawaii.edu/oc/freepubs/pdf/F_N-29.pdf

Paull, R. E., & Chen, N. J. (1987). Effect of storage temperature and wrapping on quality characteristics of litchi fruit. *Scientia Horticulturae*, *33*, 223–236. https://doi.org/10.1016/0304-4238(87)90070-7

Paull, R. E., Chen, N. J., Deputy, J., Huang, H., Cheng, G., & Gao, F. (1984). Litchi growth and compositional changes during fruit development. *Journal of the American Society for Horticultural Science*, *109*(6), 817–821. https://doi.org/10.21273/JASHS.109.6.817

Paull, R. E., Reyes, M. E. Q., & Reyes, M. U. (1995). Litchi and rambutan insect disinfestation: Treatments to minimize induced pericarp browning. *Postharvest Biology and Technology*, *6*(1–2), 139–148. https://doi.org/10.1016/0925-5214(94)00044-S

Paull, R. E., Reyes, M. E. Q., & Reyes, M. U. (1998). Sulfite residues on litchi fruit treated with sulfur dioxide. *Postharvest Biology and Technology*, *14*(2), 229–233. https://doi.org/10.1016/S0925-5214(98)00036-2

Pearson, M. A., & Miller, G. W. (2014). Benomyl. In P. Wexler (Ed.), *Encyclopedia of toxicology* (3rd ed., pp. 411–412). Academic Press. https://doi.org/10.1016/B978-0-12-386454-3.00102-0

Pesis, E., Dvir, O., Feygenberg, O., Arie, R. B., Ackerman, M., & Lichter, A. (2002). Production of acetaldehyde and ethanol during maturation and modified atmosphere storage of litchi fruit. *Postharvest Biology and Technology*, *26*(2), 157–165. https://doi.org/10.1016/S0925-5214(02)00024-8

Pornchaloempong, P., Sargent, S. A., & Fox, A. J. (1998). Controlled atmosphere storage can extend postharvest quality of lychee fruit (cv. 'Mauritius'). *Proceedings of the Florida State Horticultural Society*, *111*, 238–243. https://journals.flvc.org/fshs/issue/view/4174

Purbey, S. K., Pongener, A., Kumar, V., & Nath, V. (2018). Effect of time of harvest and packaging on quality and shelf life of litchi fruit. *Acta Horticulturae*, *1211*, 65–70. https://doi.org/10.17660/ActaHortic.2018.1211.9

Raap, U., Schaefer, T., Kapp, A., & Wedi, B. (2007). Exotic food allergy: Anaphylactic reaction to lychee. *Journal of Investigational Allergology and Clinical Immunology*, *17*(3), 199. http://www.jiaci.org/issues/vol17issue03/13.pdf

Rani, R., Ray, P. K., Barman, K., & Singh, R. R. (2018). Effect of precooling and low temperature storage on postharvest life of litchi fruits. *Acta Horticulturae*, *1211*, 227–234. https://doi.org/10.17660/ActaHortic.2018.1211.33

Reichel, M., Carle, R., Sruamsiri, P., & Neidhart, S. (2010). Influence of harvest maturity on quality and shelf-life of litchi fruit (*Litchi chinensis* Sonn.). *Postharvest Biology and Technology*, *57*(3), 162–175. https://doi.org/10.1016/j.postharvbio.2010.04.005

Reichel, M., Carle, R., Sruamsiri, P., & Neidhart, S. (2011). Changes in flavonoids and nonphenolic pigments during on-tree maturation and postharvest pericarp browning of litchi (*Litchi chinensis* Sonn.) as shown by HPLC-MS^n. *Journal of Agricultural and Food Chemistry*, *59*(8), 3924–3939. https://doi.org/10.1021/jf104432r

Reichel, M., Triani, R., Wellhöfer, J., Sruamsiri, P., Carle, R., & Neidhart, S. (2013). Vital characteristics of litchi (*Litchi chinensis* Sonn.) pericarp that define postharvest concepts for Thai cultivars. *Food and Bioprocess Technology*, *6*(5), 1191–1206. https://doi.org/10.1007/s11947-011-0762-9

Reichel, M., Wellhöfer, J., Triani, R., Sruamsiri, P., Carle, R., & Neidhart, S. (2017). Postharvest control of litchi (*Litchi chinensis* Sonn.) pericarp browning by cold storage at high relative humidity after enzyme-inhibiting treatments. *Postharvest Biology and Technology*, *125*, 77–90. https://doi.org/10.1016/j.postharvbio.2016.10.002

Revynthi, A. M., Duncan, R. E., Mannion, C., Kendra, P. E., & Carrillo, D. (2020). Post-harvest paraffinic oil dips to disinfest lychee fruit of lychee erinose mite. *Florida Entomologist*, *103*(2), 299–301. https://doi.org/10.1653/024.103.0224

Ribeiro, R. A., Mizobutsi, G. P., Finger, F. L., Puschmann, R., Vieira, G., & Moura, M. L. (2010). Influence of pH and temperature on peroxidase activity of litchi (*Litchi chinensis* Sonn.) pericarp. *Acta Horticulturae*, *864*, 323–328. https://doi.org/10.17660/ActaHortic.2010.864.43

Riederer, M., Arand, K., Burghardt, M., Huang, H., Riedel, M., Schuster, A. C., Smirnova, A., & Jiang, Y. (2015). Water loss from litchi (*Litchi chinensis*) and longan (*Dimocarpus longan*) fruits is biphasic and controlled by a complex pericarpal transpiration barrier. *Planta*, *242*(5), 1207–1219. https://doi.org/10.1007/s00425-015-2360-y

Rivera-López, J., Ordorica-Falomir, C., & Wesche-Ebeling, P. (1999). Changes in anthocyanin concentration in Lychee (*Litchi chinensis*

Sonn.) pericarp during maturation. *Food Chemistry*, *65*(2), 195–200. https://doi.org/10.1016/S0308-8146(98)00195-2

Roberts, P. B., & Follett, P. A. (2017). Food irradiation for phytosanitary and quarantine treatment. *Food irradiation technologies—Applications for preservation* (pp. 169–182). Royal Society of Chemistry. https://doi.org/10.1039/9781788010252-00169

Rodríguez, A., Alquézar, B., & Peña, L. (2013). Fruit aromas in mature fleshy fruits as signals of readiness for predation and seed dispersal. *New Phytologist*, *197*(1), 36–48. https://doi.org/10.1111/j.1469-8137.2012.04382.x

Ruenroengklin, N., Duan, X. W., Yang, B., Prasad, K. N., Cheng, G. P., Zhong, J., & Jiang, Y. M. (2008). Effects of various temperature and pH values on antioxidant activity of litchi anthocyanins. *Acta Horticulturae*, *804*, 333–338. https://doi.org/10.17660/ActaHortic.2008.804.47

Ruenroengklin, N., Sun, J., Shi, J., Xue, S. J., & Jiang, Y. (2009). Role of endogenous and exogenous phenolics in litchi anthocyanin degradation caused by polyphenol oxidase. *Food Chemistry*, *115*(4), 1253–1256. https://doi.org/10.1016/j.foodchem.2009.01.040

Ruenroengklin, N., Yang, B., Lin, H., Chen, F., & Jiang, Y. (2009). Degradation of anthocyanin from litchi fruit pericarp by H_2O_2 and hydroxyl radical. *Food Chemistry*, *116*(4), 995–998. https://doi.org/10.1016/j.foodchem.2009.03.063

Saengnil, K., Lueangprasert, K., & Uthaibutra, J. (2006). Control of enzymatic browning of harvested 'Hong Huay' litchi fruit with hot water and oxalic acid dips. *ScienceAsia*, *32*(4), 345–350. https://doi.org/10.2306/scienceasia1513-1874.2006.32.345

Saraswat, A., & Kumar, B. (2005). Anaphylactic reaction to apple, banana and lychee: What is common between botanically disparate plant families? *International Journal of Dermatology*, *44*(12), 996–998. https://doi.org/10.1111/j.1365-4632.2005.02286.x

Sarni-Manchado, P., Le Roux, E., Le Guernevé, C., Lozano, Y., & Cheynier, V. (2000). Phenolic composition of litchi fruit pericarp. *Journal of Agricultural and Food Chemistry*, *48*(12), 5995–6002. https://doi.org/10.1021/jf000815r

Saxena, S., Hajare, S. N., More, V., Kumar, S., Wadhawan, S., Mishra, B. B., Parte, M. N., Gautam, S., & Sharma, A. (2011). Antioxidant and radioprotective properties of commercially grown litchi (*Litchi chinensis*) from India. *Food Chemistry*, *126*(1), 39–45. https://doi.org/10.1016/j.foodchem.2010.10.051

Schoeman, M. H., Botha, F. A., & Kruger, F. J. (2009). Evaluation of a 'one sheet fits all carton types' SO_2 sheet on 'HLH Mauritius' and 'McLean's Red' litchi fruit. *South African Litchi Growers' Association Yearbook*, *21*, 36–39.

Schoeman, M. H., Botha, F. A., & Kruger, F. J. (2014). Evaluation of a universal slow-release sulphur dioxide sheet for the South African litchi export industry. *Acta Horticulturae*, *1029*, 359–364. https://doi.org/10.17660/ActaHortic.2014.1029.45

Schoeman, M. H., & Kruger, F. J. (2004). Refinement of SO_2 sheet application in combination with fumigation. *South African Litchi Growers' Association Yearbook*, *16*, 4–9.

Schoeman, M. H., Lemmer, D., & Kruger, F. J. (2008). Preliminary evaluation of SO_2 sheets to prevent postharvest diseases of South African export litchi fruit. *South African Litchi Growers' Association Yearbook*, *20*, 6–9.

Schoeman, M. H., Penter, M., & Kruger, F. J. (2004). Determination of maturity cut-off points for South African export litchi fruit. *South African Litchi Growers' Association Yearbook*, *16*, 14–20.

Schutte, G. C., Botha, T., & Kotze, J. M. (1990). Postharvest control of decay and browning of litchi fruit by fungicide dips and paper sheets impregnated with sodium metabisulphite. *South African Litchi Growers' Association Yearbook*, *3*, 10–14.

Scott, K. J., Brown, B. I., Chaplin, G. R., Wilcox, M. E., & Bain, J. M. (1982). The control of rotting and browning of litchi fruit by hot benomyl and plastic film. *Scientia Horticulturae*, *16*(3), 253–262. https://doi.org/10.1016/0304-4238(82)90073-5

Septembre-Malaterre, A., Stanislas, G., Douraguia, E., & Gonthier, M. P. (2016). Evaluation of nutritional and antioxidant properties of the tropical fruits banana, litchi, mango, papaya, passion fruit and pineapple cultivated in Réunion French Island. *Food Chemistry*, *212*, 225–233. https://doi.org/10.1016/j.foodchem.2016.05.147

Shah, H. M. S., Khan, A. S., & Ali, S. (2017). Pre-storage kojic acid application delays pericarp browning and maintains antioxidant activities of litchi fruit. *Postharvest Biology and Technology*, *132*, 154–161. https://doi.org/10.1016/j.postharvbio.2017.06.004

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 level. *Acta Horticulturae*, *804*, 339–346. https://doi.org/10.17660/ActaHortic.2008.804.48

Singh, A., Abidi, A. B., & Srivastava, S. (1987). Variation in quality traits of litchi (*Litchi chinensis* Sonn.) cultivars. *Journal of Food Science and Technology*, *24*(5), 264–266.

Singh, S. P., Saini, M. K., Singh, J., Pongener, A., & Sidhu, G. S. (2014). Preharvest application of abscisic acid promotes anthocyanins accumulation in pericarp of litchi fruit without adversely affecting postharvest quality. *Postharvest Biology and Technology*, *96*, 14–22. https://doi.org/10.1016/j.postharvbio.2014.05.005

Sittigul, C., Sardsud, U., Sardsud, V., & Chaiwangsri, T. (1994). Effects of fruit maturity at harvest on disease development in lychee during storage. In G. I. Johnson, & E. Highley (Eds.), *Development of postharvest handling technology for tropical tree fruits* (pp. 9–14). Proceedings Australian Centre for International Agricultural Research (ACIAR). https://www.aciar.gov.au/publication/technical-publications/development-postharvest-handling-technology-tropical-tree-fruits

Sivakumar, D., Arrebola, E., & Korsten, L. (2008). Postharvest decay control and quality retention in litchi (cv. 'McLean's Red') by combined application of modified atmosphere packaging and antimicrobial agents. *Crop Protection*, *27*, 1208–1214. https://doi.org/10.1016/j.cropro.2008.03.002

Sivakumar, D., & Korsten, L. (2004). A preliminary study on the changes of epicuticular wax layer of litchi (cv. 'Mauritius') with respect to commercial packing line operations. *South African Litchi Growers' Association Yearbook*, *16*, 31–33.

Sivakumar, D., & Korsten, L. (2005). Preliminary observations of preharvest micro-cracking development in the pericarp of litchi cv. 'Mauritius'. *South African Litchi Growers' Association Yearbook*, *17*, 34–36.

Sivakumar, D., & Korsten, L. (2006a). Evaluation of the integrated application of two types of modified atmosphere packaging and hot water treatments on quality retention in the litchi cultivar 'McLean's Red'. *The Journal of Horticultural Science and Biotechnology*, *81*(4), 639–644. https://doi.org/10.1080/14620316.2006.11512117

Sivakumar, D., & Korsten, L. (2006b). Influence of modified atmosphere packaging and postharvest treatments on quality retention of litchi cv. Mauritius. *Postharvest Biology and Technology*, *41*(2), 135–142. https://doi.org/10.1016/j.postharvbio.2006.03.007

Sivakumar, D., & Korsten, L. (2010). Fruit quality and physiological responses of litchi cultivar McLean's Red to 1-methylcyclopropene

pre-treatment and controlled atmosphere storage conditions. *LWT—Food Science and Technology*, *43*(6), 942–948. https://doi.org/10.1016/j.lwt.2010.02.001

Sivakumar, D., Naudé, Y., Rohwer, E., & Korsten, L. (2008). Volatile compounds, quality attributes, mineral composition and pericarp structure of South African litchi export cultivars Mauritius and McLean's Red. *Journal of the Science of Food and Agriculture*, *88*(6), 1074–1081. https://doi.org/10.1002/jsfa.3201

Sivakumar, D., Regnier, T., Demoz, B., & Korsten, L. (2005). Effect of different post-harvest treatments on overall quality retention in litchi fruit during low temperature storage. *The Journal of Horticultural Science and Biotechnology*, *80*(1), 32–38. https://doi.org/10.1080/14620316.2005.11511887

Sivakumar, D., Terry, L. A., & Korsten, L. (2010). An overview on litchi fruit quality and alternative postharvest treatments to replace sulfur dioxide fumigation. *Food Reviews International*, *26*(2), 162–188. https://doi.org/10.1080/87559121003590516

Sivakumar, D., Zeeman, K., & Korsten, L. (2007). Effect of a biocontrol agent (*Bacillus subtilis*) and modified atmosphere packaging on postharvest decay control and quality retention of litchi during storage. *Phytoparasitica*, *35*(5), 507–518. https://doi.org/10.1007/BF03020609

Somboonkaew, N., & Terry, L. A. (2010). Deterioration of anthocyanins in litchi 'Kom' Fruit stored under different relative humidity levels. *Acta Horticulturae*, *863*, 443–448. https://doi.org/10.17660/ActaHortic.2010.863.60

Song, J. J., Zhang, H. Y., Liu, Z. G., & Ran, P. X. (2007). Cloning of the panallergen profilin from lychee fruit and its cross-reactivity with birch pollen profilin Bet v 2. *Food and Agricultural Immunology*, *18*(2), 129–138. https://doi.org/10.1080/09540100701616290

South African Litchi Growers' Association Website. (2020). *Harvesting and post-harvest treatments for litchis*. http://southafrica.co.za/management-practices-for-litchis.html

Stern, A. R., Nerya, O., & Ben-Arie, R. (2006). The cytokinin CPPU delays maturity in litchi cv. 'Mauritius' and extends storage-life. *The Journal of Horticultural Science and Biotechnology*, *81*(1), 158–162. https://doi.org/10.1080/14620316.2006.11512043

Stern, R. A., Adato, I., Goren, M., Eisenstein, D., & Gazit, S. (1993). Effects of autumnal water stress on litchi flowering and yield in Israel. *Scientia Horticulturae*, *54*(4), 295–302. https://doi.org/10.1016/0304-4238(93)90108-3

Stern, R. A., & Gazit, S. (1996). Lychee pollination by the honeybee. *Journal of the American Society for Horticultural Science*, *121*(1), 152–157. https://doi.org/10.21273/JASHS.121.1.152

Su, D., Ti, H., Zhang, R., Zhang, M., Wei, Z., Deng, Y., & Guo, J. (2014). Structural elucidation and cellular antioxidant activity evaluation of major antioxidant phenolics in lychee pulp. *Food Chemistry*, *158*, 385–391. https://doi.org/10.1016/j.foodchem.2014.02.134

Su, Z., Hu, M., Gao, Z., Li, M., Yun, Z., Pan, Y., Zhang, Z., & Jiang, Y. (2019). Apple polyphenols delay senescence and maintain edible quality in litchi fruit during storage. *Postharvest Biology and Technology*, *157*, 110976. https://doi.org/10.1016/j.postharvbio.2019.110976

Sultan, M. Z. (2014). Effect of postharvest coating with gum arabic on pericarp browning and desiccation of litchi fruit (*Litchi chinensis* Sonn.) during storage. *Acta Horticulturae*, *1029*, 345–351. https://doi.org/10.17660/ActaHortic.2014.1029.43

Sun, D., Liang, G., Xie, J., Lei, X., & Mo, Y. (2010). Improved preservation effects of litchi fruit by combining chitosan coating with ascorbic acid treatment during postharvest storage. *African Journal of Biotechnology*, *9*(22), 3272–3279. https://www.ajol.info/index.php/ajb/article/view/80657

Sun, J., Jiang, Y., Shi, J., Wei, X., Xue, S. J., Shi, J., & Yi, C. (2010). Antioxidant activities and contents of polyphenol oxidase substrates from pericarp tissues of litchi fruit. *Food Chemistry*, *119*(2), 753–757. https://doi.org/10.1016/j.foodchem.2009.07.025

Sun, J., Jiang, Y., Wei, X., Shi, J., You, Y., Liu, H., Kakuda, Y., & Zhao, M. (2006). Identification of (−)-epicatechin as the direct substrate for polyphenol oxidase isolated from litchi pericarp. *Food Research International*, *39*(8), 864–870. https://doi.org/10.1016/j.foodres.2006.05.001

Sun, J., Li, C., Prasad, K. N., You, X., Li, L., Liao, F., Peng, H., He, X., Li, Z., & Zhang, Y. (2012). Membrane deterioration, enzymatic browning and oxidative stress in fresh fruits of three litchi cultivars during six-day storage. *Scientia Horticulturae*, *148*, 97–103. https://doi.org/10.1016/j.scienta.2012.09.023

Sun, J., Xiang, X., Yu, C., Shi, J., Peng, H., Yang, B., Yang, S., & Jiang, Y. (2009). Variations in contents of browning substrates and activities of some related enzymes during litchi fruit development. *Scientia Horticulturae*, *120*(4), 555–559. https://doi.org/10.1016/j.scienta.2008.12.006

Sun, J., You, X., Li, L., Peng, H., Su, W., Li, C., He, Q., & Liao, F. (2011). Effects of a phospholipase D inhibitor on postharvest enzymatic browning and oxidative stress of litchi fruit. *Postharvest Biology and Technology*, *62*(3), 288–294. https://doi.org/10.1016/j.postharvbio.2011.07.001

Swarts, D. H. (1983). *Postharvest handling of litchis*. Farming in South Africa. Department of Agriculture, Pretoria, South Africa.

Swarts, D. H. (1985). Sulphur content of fumigated South African litchi fruit. *Subtropica*, *6*(7), 22–24.

Swarts, D. H., & Anderson, T. (1980). *Chemical control of mould growth on litchis during storage and sea shipment* (Information bulletin). Citrus and Subtropical Fruit Research Institute.

Tan, X. J., & Li, Y. B. (1984). The partial purification and properties of polyphenol oxidase from the pericarp of litchi (Litchi chinensis). *Acta Phytophysiology Sinica*, *10*, 339–345. (In Chinese with English abstract).

Tan, X. J., & Zhou, Y. C. (1987). Studies on the enzymatic browning of *Litchi chinensis* pericarp by polyphenol oxidase. *Acta Phytophysiologica Sinica*, *13*(2), 197–203. (In Chinese with English abstract).

Tang, R., Zhou, Y., Chen, Z., Wang, L., Lai, Y., Chang, S. K., Wang, Y. F., Qu, H. X., Jiang, Y. M., & Huang, H. (2020). Regulation of browning and senescence of litchi fruit mediated by phenolics and energy status: A postharvest comparison on three different cultivars. *Postharvest Biology and Technology*, *168*, 111280. https://doi.org/10.1016/j.postharvbio.2020.111280

Techavuthiporn, C., Nivomlao, W., & Kanlavanarat, S. (2006). Superatmospheric oxygen retards pericarp browning of litchi cv. Hong Huay. *Acta Horticulturae*, *712*, 629–634. https://doi.org/10.17660/ActaHortic.2006.712.77

Terdbaramee, U., Ratanakhanokchai, K., & Kanlayanarat, S. (2003). Effect of citric acid on the control of postharvest browning of lychee fruit under cold storage. *Acta Horticulturae*, *628*, 527–532. https://doi.org/10.17660/ActaHortic.2003.628.66

Tholl, D. (2006). Terpene synthases and the regulation, diversity and biological roles of terpene metabolism. *Current Opinion in Plant Biology*, *9*(3), 297–304. https://doi.org/10.1016/j.pbi.2006.03.014

Tian, S. P., Li, B. Q., & Xu, Y. (2005). Effects of O_2 and CO_2 concentrations on physiology and quality of litchi fruit in storage. *Food Chemistry*, *91*(4), 659–663. https://doi.org/10.1016/j.foodchem.2004.06.038

Tiffney, B. H. (2004). Vertebrate dispersal of seed plants through time. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 1–29. https://doi.org/10.1146/annurev.ecolsys.34.011802.132535

Timberlake, C. F., & Bridle, P. (1967). Flavylium salts, anthocyanidins and anthocyanins II. Reactions with sulphur dioxide. *Journal of the Science of Food and Agriculture*, *18*(10), 479–485. https://doi.org/10.1002/jsfa.2740181009

Tongdee, S. C. (1992). Postharvest handling and technology of tropical fruit. *Acta Horticulturae*, *321*, 713–717. https://doi.org/10.17660/ActaHortic.1992.321.89

Tongdee, S. C. (1994). Sulphur dioxide fumigation in postharvest-handling of fresh longan and lychee for export. In B. R. Champ, E. Highley, & G. I. Johnson (Eds.), *Postharvest handling of tropical fruits: Proceedings of an international conference held at Chiang Mai, Thailand, 19–23 July 1993. ACIAR proceedings No. 50* (pp. 186–195). ACIAR. https://www.aciar.gov.au/sites/default/files/legacy/node/2248/pr50_pdf_70186.pdf

Tongdee, S. C. (1998). Postharvest technology of fresh lychee: Commercial perspectives from Thailand. *South African Litchi Growers' Association Yearbook*, *9*, 37–43.

Tongdee, S. C., McGlasson, W. B., & Scott, K. J. (1982). Packaging and cool storage of litchi fruit. *CSIRO Food Research Quarterly (Australia)*, *42*, 25–28.

Toulemonde, B., & Beauverd, D. (1985). Headspace analysis: Trap desorption by microwave energy application to the volatile components of some tropical fruits. In *Progress in flavour research proceedings of the 4th weurman flavour research symposium, Dourdan, France, 9–11 May, 1984* (pp. 533–548). Developments in Food Science. University of Chicago.

Trias Mansilla, R., Bañeras Vives, L., Montesinos Seguí, E., & Badosa Romañó, E. (2008). Lactic acid bacteria from fresh fruit and vegetables as biocontrol agents of phytopathogenic bacteria and fungi. *International Microbiology*, *11*, 231–236. https://doi.org/10.2436/20.1501.01.66

Tripathi, V. K., Kaphalia, B. S., Seth, T. D., & Surjeet, S. (1987). Composition of litchi cultivars. *Indian Food Packer*, *41*(4), 7–10.

Underhill, S. J., & Critchley, C. (1994). Anthocyanin decolorisation and its role in lychee pericarp browning. *Australian Journal of Experimental Agriculture*, *34*(1), 115–122. https://doi.org/10.1071/EA9940115

Underhill, S. J., Bagshaw, J., Prasad, A., Zauberman, G., Ronen, R., & Fuchs, Y. (1992). The control of lychee (*Litchi chinensis* Sonn.) postharvest skin browning using sulphur dioxide and low pH. *Acta Horticulturae*, *321*, 732–741. https://doi.org/10.17660/ActaHortic.1992.321.92

Underhill, S. J., & Critchley, C. (1992). The physiology and anatomy of lychee (*Litchi chinensis* Sonn.) pericarp during fruit development. *Journal of Horticultural Science*, *67*(4), 437–444. https://doi.org/10.1080/00221589.1992.11516269

Underhill, S. J., & Critchley, C. (1993a). Lychee pericarp browning caused by heat injury. *HortScience*, *28*(7), 721–722. https://doi.org/10.21273/HORTSCI.28.7.721

Underhill, S. J., & Critchley, C. (1993b). Physiological, biochemical and anatomical changes in lychee (*Litchi chinensis* Sonn.) pericarp during storage. *Journal of Horticultural Science*, *68*(3), 327–335. https://doi.org/10.1080/00221589.1993.11516358

Underhill, S. J., & Critchley, C. (1995). Cellular localisation of polyphenol oxidase and peroxidase activity in *Litchi chinensis* Sonn. pericarp. *Functional Plant Biology*, *22*(4), 627–632. https://doi.org/10.1071/PP9950627

Underhill, S. J., & Simons, D. H. (1993). Lychee (*Litchi chinensis* Sonn.) pericarp desiccation and the importance of postharvest microcracking. *Scientia Horticulturae*, *54*(4), 287–294. https://doi.org/10.1016/0304-4238(93)90107-2

Underhill, S. J., Simons, D. H., & Critchley, C. (1992). Postharvest pericarp browning of lychee (*Litchi chinensis* Sonn.) fruit. *Acta Horticulturae*, *321*, 718–725. https://doi.org/10.17660/ActaHortic.1992.321.90

Underhill, S. J. R., & Wong, L. S. (1990). A maturity standard for lychee (*Litchi chinensis* Sonn.). *Acta Horticulturae*, *269*, 181–187. https://doi.org/10.17660/ActaHortic.1990.269.23

Underhill, S. J. R. (1992). Lychee (*Litchi chinensis* Sonn.) pericarp browning. *Tropical Science*, *32*, 305–312.

Underhill, S. J. R. (1994). An overview of lychee postharvest technology. In G. I. Johnson & E. Highley (Eds.), *Development of postharvest handling technology for tropical tree fruits* (pp. 36–40). Proceedings Australian Centre for International Agricultural Research (ACIAR). https://www.aciar.gov.au/publication/technical-publications/development-postharvest-handling-technology-tropical-tree-fruits

Underhill, S. J. R., Gardiner, S., & Prasad, A. (1994). The use of sulfur dioxide and low pH treatment to control lychee (*Litchi chinensis* Sonn.) pericarp browning. In G. I. Johnson & E. Highley (Eds.), *Development of postharvest handling technology for tropical tree fruits* (pp. 30–35). Proceedings Australian Centre for International Agricultural Research (ACIAR). https://www.aciar.gov.au/publication/technical-publications/development-postharvest-handling-technology-tropical-tree-fruits

USDA. (2016). *FoodData central*. USDA. https://fdc.nal.usda.gov

Valenta, K., Burke, R. J., Styler, S. A., Jackson, D. A., Melin, A. D., & Lehman, S. M. (2013). Colour and odour drive fruit selection and seed dispersal by mouse lemurs. *Scientific Reports*, *3*(1), 1–5. https://doi.org/10.1038/srep02424

Vigneault, C., Bartz, J. A., & Sargent, S. A. (2000). Postharvest decay risk associated with hydrocooling tomatoes. *Plant Disease*, *84*(12), 1314–1318. https://doi.org/10.1094/PDIS.2000.84.12.1314

Vilasachandran, T., & Sargent, S. A. (1997). Postharvest quality of lychee fruit: Role of relative humidity and panicle. *HortScience*, *32*, 433–433. https://doi.org/10.21273/HORTSCI.32.3.433D

Wall, M. M. (2006). Ascorbic acid and mineral composition of longan (*Dimocarpus longan*), lychee (*Litchi chinensis*) and rambutan (*Nephelium lappaceum*) cultivars grown in Hawaii. *Journal of Food Composition and Analysis*, *19*, 655–663. https://doi.org/10.1016/j.jfca.2005.12.001

Wall, M. M. (2008). Quality of postharvest horticultural crops after irradiation treatment. *Stewart Postharvest Review*, *4*(2), 1–7. https://doi.org/10.2212/spr.2008.2.1

Wang, C. Y., Chen, H., Jin, P., & Gao, H. (2010). Maintaining quality of litchi fruit with acidified calcium sulfate. *Journal of Agricultural and Food Chemistry*, *58*(15), 8658–8666. https://doi.org/10.1021/jf100607e

Wang, H., Huang, H., & Huang, X. (2003). Sugar accumulation and related enzyme activities in the litchi fruit of 'Nuomici' and

'Feizixiao'. *Acta Horticulturae Sinica*, *30*(1), 1–5. (In Chinese with English abstract).

Wang, H., Huang, H., & Huang, X. (2007). Differential effects of abscisic acid and ethylene on the fruit maturation of *Litchi chinensis* Sonn. *Plant Growth Regulation*, *52*(3), 189–198. https://doi.org/10.1007/s10725-007-9189-8

Wang, H., Qian, Z., Ma, S., Zhou, Y., Patrick, J. W., Duan, X., Jiang, Y. M., & Qu, H. (2013). Energy status of ripening and postharvest senescent fruit of litchi (*Litchi chinensis* Sonn.). *BMC Plant Biology*, *13*(1), 1–16. http://www.biomedcentral.com/1471-2229/13/55 https://doi.org/10.1186/1471-2229-13-55

Wang, H. C., Hu, Z. Q., Wang, Y., Chen, H. B., & Huang, X. M. (2011). Phenolic compounds and the antioxidant activities in litchi pericarp: Difference among cultivars. *Scientia Horticulturae*, *129*(4), 784–789. https://doi.org/10.1016/j.scienta.2011.05.042

Wang, H. C., Huang, H. B., Huang, X. M., & Hu, Z. Q. (2006). Sugar and acid compositions in the arils of *Litchi chinensis* Sonn.: Cultivar differences and evidence for the absence of succinic acid. *The Journal of Horticultural Science and Biotechnology*, *81*(1), 57–62. https://doi.org/10.1080/14620316.2006.11512029

Wang, H. C., Huang, X. M., & Huang, H. B. (2001). Litchi fruit maturation studies: Changes in abscisic acid and 1-aminocyclopropane-1-carboxylic acid and the effects of cytokinin and ethylene on coloration in cv. Feizixiao. *Acta Horticulturae*, *558*, 267–271. https://doi.org/10.17660/ActaHortic.2001.558.42

Wang, H. C., Lai, B., & Huang, X. M. (2017). Litchi fruit set, development, and maturation. In M. Kumar, V. Kumar, R. Prasad, & A. Varma (Eds.), *The lychee biotechnology* (pp. 1–30). Springer. https://doi.org/10.1007/978-981-10-3644-6_1

Wang, J., Liu, B., Xiao, Q., Li, H., & Sun, J. (2014). Cloning and expression analysis of litchi (*Litchi Chinensis* Sonn.) polyphenol oxidase gene and relationship with postharvest pericarp browning. *PLoS One*, *9*(4), e93982. https://doi.org/10.1371/journal.pone.0093982

Wang, J., Wang, X., Xu, B., & Jin, Z. (2010). Physiological changes during the process of pericarp browning in the postharvest litchi. *Agricultural Science & Technology-Hunan*, *11*(5), 10–16. https://www.cabdirect.org/cabdirect/FullTextPDF/2010/20103342789.pdf

Wang, J. B., Wang, X. S., & Jin, Z. Q. (2010). Enzymatic browning of postharvest litchi: A review. *Acta Horticulturae*, *863*, 613–618. https://doi.org/10.17660/ActaHortic.2010.863.86

Wang, T., Hu, M., Yuan, D., Yun, Z., Gao, Z., Su, Z., & Zhang, Z. (2020). Melatonin alleviates pericarp browning in litchi fruit by regulating membrane lipid and energy metabolisms. *Postharvest Biology and Technology*, *160*, 111066. https://doi.org/10.1016/j.postharvbio.2019.111066

Wang, X., Hu, X., Yan, H., Ma, Z., & Deng, X. (2016). Pro-inflammatory effects of a litchi protein extract in murine RAW264.7 macrophages. *Horticulture Research*, *3*, 16017. https://doi.org/10.1038/hortres.2017.59

Wang, Y., Wang, H., Zhou, Z., Chen, H., Hu, G., & Huang, X. (2009). An overview of research on litchi functional role and its active substances. *Journal of Fruit Science*, *26*(4), 546–552. (In Chinese with English Abstract).

Watt, B. K., & Merril, A. L. (1963). *Composition of foods; Raw, processed, prepared*. USDA.

Watt, B. K., & Merril, A. L. (1975). *Composition of foods: Raw, processed, prepared*. Consumer and Food Economics Institute, Agricultural Research Service, US Department of Agriculture.

Wei, Y. Z., Hu, F. C., Hu, G. B., Li, X. J., Huang, X. M., & Wang, H. C. (2011). Differential expression of anthocyanin biosynthetic genes in relation to anthocyanin accumulation in the pericarp of *Litchi chinensis* Sonn. *PLoS One*, *6*(4), 1–11. https://doi.org/10.1371/journal.pone.0019455

Wenkam, N. S. (1990). *Foods of Hawaii and the Pacific Basin. Fruits and fruit products: Raw, processed and prepared* (Vol. 4). College of Tropical Agriculture and Human Resources, Research Extension Series #110. http://hdl.handle.net/10125/5492

Wermund, U., Goyard, J., Jahiel, M., & Ohmayer, G. (2014). The effect of different fumigation protocols and packaging material on litchi fruit from Madagascar with regard to quality and shelf life. *Acta Horticulturae*, *102*, 371–377. https://doi.org/10.17660/ActaHortic.2014.1029.47

Wermund, U., Goyard, J., Reeber, T., Bostel, A., & Ohmayer, G. (2014). Evaluation of different SO_2 analysis methods on litchi fruit. *Acta Horticulturae*, *1029*, 365–369. https://doi.org/10.17660/ActaHortic.2014.1029.46

Wong, L. S., Jacobi, K. K., & Giles, J. E. (1991). The influence of hot benomyl dips on the appearance of cool stored lychee (*Litchi chinensis* Sonn.). *Scientia Horticulturae*, *46*(3–4), 245–251. https://doi.org/10.1016/0304-4238(91)90047-3

Wu, M. X., Ji, Z. L., Chen, W. X., Han, D. M., & Wu, Z. X. (2001). A study of the behavior of 'Feizixiao' litchi during storage. *Acta Horticulturae*, *558*, 381–386. https://doi.org/10.17660/ActaHortic.2001.558.61

Wu, Y., Lin, H., Lin, Y., Shi, J., Xue, S., Hung, Y. C., Chen, Y. H., & Wang, H. (2017). Effects of biocontrol bacteria *Bacillus amyloliquefaciens* LY-1 culture broth on quality attributes and storability of harvested litchi fruit. *Postharvest Biology and Technology*, *132*, 81–87. https://doi.org/10.1016/j.postharvbio.2017.05.021

Wu, Y., Pan, Q., Qu, W., & Duan, C. (2009). Comparison of volatile profiles of nine litchi (*Litchi chinensis* Sonn.) cultivars from Southern China. *Journal of Agricultural and Food Chemistry*, *57*(20), 9676–9681. https://doi.org/10.1021/jf902144c

Wu, Z., Su, M., Chen, W., & Hu, G. (1998). Studies on polyphenol oxidase and peroxidase and litchi pericarp browning during storage. *Hua nan Nong ye da xue xue bao. Journal of South China Agricultural University*, *19*(1), 12–15. (In Chinese with English abstract).

Wu, Z. C., Yang, Z. Y., Li, J. G., Chen, H. B., Huang, X. M., & Wang, H. C. (2016). Methyl-inositol, γ-aminobutyric acid and other health benefit compounds in the aril of litchi. *International Journal of Food Sciences and Nutrition*, *67*(7), 762–772. https://doi.org/10.1080/09637486.2016.1198888

Xiao, L., Li, T., Jiang, G., John, A., Zhang, D., Jin, W., Duan, X., & Jiang, Y. (2019). Effects of dry fog humidification on pericarp browning and quality of litchi fruit stored at low temperature. *International Journal of Agricultural and Biological Engineering*, *12*(4), 192–196. https://doi.org/10.25165/j.ijabe.20191204.4420

Xiao, Q., Feng, C., Liu, B. H., Li, H. L., Zhang, X. C., Du, Z. J., & Wang, J. B. (2011). A comparative study on changes in membrane lipid super oxidization and related enzyme activities during postharvest pericarp browning in different litchi cultivars. *Chinese Journal of Tropical Crops*, *32*(9), 1653–1657. (In Chinese with English abstract).

Xu, S., Lu, H., & Sun, X. (2020). Quality detection of postharvest litchi based on electronic nose: A feasible way for litchi fruit supervision during circulation process. *HortScience*, *55*(4), 476–482. https://doi.org/10.21273/HORTSCI14750-19

Xu, X., Wu, Z., Chen, W., & Su, M. (2005). Effect of low temperature on relative enzyme activity and membrane peroxidization of lychee fruits. *Acta Horticulturae*, *665*, 359–364. https://doi.org/10.17660/ActaHortic.2005.665.44

Yang, S., Feng, L., Yang, E., Chen, Y., Dong, X., Su, X., & Jiang, Y. (2011). Lipofuscin-Like substance involved in pericarp browning of postharvest litchi fruit during storage. *The Open Food Science Journal*, *5*(1), 47–50. https://doi.org/10.2174/1874256401105010047

Yang, Y., Han, Y., Meng, X., Wang, Y., Li, K., Xu, S., & Yang, Y. (2019). Effect of composite antimicrobial coating containing cinnamaldehyde on postharvest preservation of litchi fruit. *Shipin Kexue/Food Science*, *40*(23), 253–261. https://doi.org/10.7506/spkx1002-6630-20181026-316

Yang, Z., Wang, T., Wang, H., Huang, X., Qin, Y., & Hu, G. (2013). Patterns of enzyme activities and gene expressions in sucrose metabolism in relation to sugar accumulation and composition in the aril of *Litchi chinensis* Sonn. *Journal of Plant Physiology*, *170*(8), 731–740. https://doi.org/10.1016/j.jplph.2012.12.021

Yen, C. R. (1983). Variation in fruit characters between normal-and shrivelled-seed lychee varieties. *Journal of Agriculture Research, China*, *32*(1), 39–49. https://scholars.tari.gov.tw/handle/123456789/12905

Yen, C. R. (1984). Seeded and seedless fruits growth of 'Sah Keng' litchi. *Journal of Agriculture Research, China*, *33*(3), 257–264. https://scholars.tari.gov.tw/handle/123456789/13943

Yi, C., Jiang, Y., Shi, J., Qu, H., Xue, S., Duan, X., Shi, J., & Prasad, N. K. (2010). ATP-regulation of antioxidant properties and phenolics in litchi fruit during browning and pathogen infection process. *Food Chemistry*, *118*(1), 42–47. https://doi.org/10.1016/j.foodchem.2009.04.074

Yi, C., Qu, H. X., Jiang, Y. M., Duan, X. W., Cheng, G. P., Ruenroengklin, N., & Yang, E. (2008). Roles of energy in senescence and disease development of harvested litchi fruit. *Acta Horticulturae*, *804*, 347–353. https://doi.org/10.17660/ActaHortic.2008.804.49

Yi, C., Qu, H. X., Jiang, Y. M., Shi, J., Duan, X. W., Joyce, D. C., & Li, Y. B. (2008). ATP-induced changes in energy status and membrane integrity of harvested litchi fruit and its relation to pathogen resistance. *Journal of Phytopathology*, *156*(6), 365–371. https://doi.org/10.1111/j.1439-0434.2007.01371.x

Yin, J. H., Gao, F. F., Hu, G. B., & Zhu, S. H. (2001). The regulation of litchi maturation and coloration by abscisic acid and ethylene. *Acta Horticulturae*, *558*, 293–296. https://doi.org/10.17660/ActaHortic.2001.558.47

Yun, Z., Gao, H., Chen, X., Chen, Z., Zhang, Z., Li, T., Qu, H. X., & Jiang, Y. (2021). Effects of hydrogen water treatment on antioxidant system of litchi fruit during the pericarp browning. *Food Chemistry*, *336*, 127618. https://doi.org/10.1016/j.foodchem.2020.127618

Yun, Z., Qu, H., Wang, H., Zhu, F., Zhang, Z., Duan, X., Yang, B., Chen, Y., & Jiang, Y. (2016). Comparative transcriptome and metabolome provide new insights into the regulatory mechanisms of accelerated senescence in litchi fruit after cold storage. *Scientific Reports*, *6*(1), 1–16. https://doi.org/10.1038/srep19356

Zauberman, G., Ronen, R., Akerman, M., & Fuchs, Y. (1990). Low pH treatment protects litchi fruit color. *Acta Horticulturae*, *269*, 309–314. https://doi.org/10.17660/ActaHortic.1990.269.41

Zauberman, G., Ronen, R., Akerman, M., Weksler, A., Rot, I., & Fuchs, Y. (1991). Post-harvest retention of the red colour of litchi fruit pericarp. *Scientia Horticulturae*, *47*(1–2), 89–97. https://doi.org/10.1016/0304-4238(91)90030-3

Zeng, L., Liao, J., & Chen, H. (2012). Effects of glutamic acid and TDZ (Thidiazuron) on the fruit coloration and quality of *Litchi chinensis* Sonn. *Journal of Tropical and Subtropical Botany*, *20*(4), 382–387. https://doi.org/10.3969/j.issn.1005-3395.2012.04.010

Zhang, D., & Quantick, P. C. (1997). Effects of chitosan coating on enzymatic browning and decay during postharvest storage of litchi (*Litchi chinensis* Sonn.) fruit. *Postharvest Biology and Technology*, *12*(2), 195–202. https://doi.org/10.1016/S0925-5214(97)00057-4

Zhang, D., Quantick, P. C., & Grigor, J. M. (2000). Changes in phenolic compounds in Litchi (*Litchi chinensis* Sonn.) fruit during postharvest storage. *Postharvest Biology and Technology*, *19*(2), 165–172. https://doi.org/10.1016/S0925-5214(00)00084-3

Zhang, D., Xu, X., Zhang, Z., Jiang, G., Feng, L., Duan, X., & Jiang, Y. (2018). 6-Benzylaminopurine improves the quality of harvested litchi fruit. *Postharvest Biology and Technology*, *143*, 137–142. https://doi.org/10.1016/j.postharvbio.2018.05.002

Zhang, H. N., Li, W. C., Wang, H. C., Shi, S. Y., Shu, B., Liu, L. Q., Wei, Y. Z., & Xie, J. H. (2016). Transcriptome profiling of light-regulated anthocyanin biosynthesis in the pericarp of litchi. *Frontiers in Plant Science*, *7*, 963. https://doi.org/10.3389/fpls.2016.00963

Zhang, J., Wu, Z., Hu, F., Liu, L., Huang, X., Zhao, J., & Wang, H. (2018). Aberrant seed development in *Litchi chinensis* is associated with the impaired expression of cell wall invertase genes. *Horticulture Research*, *5*, 39. https://doi.org/10.1038/s41438-018-0042-1

Zhang, J. P., Jia, C. H., Wang, J. B, & Xu, B. Y. (2014). Expression analysis and determination of enzyme activity of the glutathione transferase gene from postharvest litchi pericarp. *热带作物学报Chinese Journal of Tropical Crops*, *35*(12), 2368–2373. (In Chinese with English abstract). http://www.rdzwxb.com/EN/Y2014/V35/I12/2368

Zhang, R., Zeng, Q., Deng, Y., Zhang, M., Wei, Z., Zhang, Y., & Tang, X. (2013). Phenolic profiles and antioxidant activity of litchi pulp of different cultivars cultivated in Southern China. *Food Chemistry*, *136*(3–4), 1169–1176. https://doi.org/10.1016/j.foodchem.2012.09.085

Zhang, Y., Huber, D. J., Hu, M., Jiang, G., Gao, Z., Xu, X., Jiang, Y., & Zhang, Z. (2018). Delay of postharvest browning in litchi fruit by melatonin via the enhancing of antioxidative processes and oxidation repair. *Journal of Agricultural and Food Chemistry*, *66*(28), 7475–7484. https://doi.org/10.1021/acs.jafc.8b01922

Zhang, Z., Dvir, O., Pesis, E., Pick, U., & Lichter, A. (2005). Weak organic acids and inhibitors of pH homeostasis suppress growth of Penicillium infesting litchi fruits. *Journal of Phytopathology*, *153*(11–12), 667–673. https://doi.org/10.1111/j.1439-0434.2005.01034.x

Zhang, Z., Hu, M., Yun, Z., Wang, J., Feng, G., Gao, Z., Shi, X., & Jiang, Y. (2017). Effect of tea seed oil treatment on browning of litchi fruit in relation to energy status and metabolism. *Postharvest Biology and Technology*, *132*, 97–104. https://doi.org/10.1016/j.postharvbio.2017.05.010

Zhang, Z., Huber, D. J., Qu, H., Yun, Z. E., Wang, H., Huang, Z., Huang, H., & Jiang, Y. (2015). Enzymatic browning and antioxidant activities in harvested litchi fruit as influenced by apple polyphenols. *Food Chemistry*, *171*, 191–199. https://doi.org/10.1016/j.foodchem.2014.09.001

Zhang, Z., Pang, X., Duan, X., & Ji, Z. (2002). Change of anthocyanin content and its determination during lychee pericarp browning. *Journal of South China Agricultural University*, *23*(1), 16–19. (In Chinese with English abstract). https://doi.org/10.7671/j.issn.1001-411X.2002.01.005

Zhang, Z., Pang, X., Ji, Z., & Jiang, Y. (2001). Role of anthocyanin degradation in litchi pericarp browning. *Food Chemistry*, *75*(2), 217–221. https://doi.org/10.1016/S0308-8146(01)00202-3

Zhang, Z., Pang, X., Xuewu, D., Ji, Z., & Jiang, Y. (2005). Role of peroxidase in anthocyanin degradation in litchi fruit pericarp. *Food Chemistry*, *90*(1–2), 47–52. https://doi.org/10.1016/j.foodchem.2004.03.023

Zhang, Z., Xuequn, P., Yang, C., Ji, Z., & Jiang, Y. (2004). Purification and structural analysis of anthocyanins from litchi pericarp. *Food Chemistry*, *84*(4), 601–604. https://doi.org/10.1016/j.foodchem.2003.05.002

Zhang, Z. Q., Pang, X. Q., Duan, X. W., & Ji, Z. L. (2003). The anthocyanin degradation and anthocyanase activity during the pericarp browning of lychee fruit. *Scientia Agricultura Sinica*, *36*(8), 945–949. (In Chinese with English abstract). https://www.chinaagrisci.com/CN/Y2003/V36/I8/945

Zhang, Z. Q., Pang, X. Q., Ji, Z. L., & Li, X. P. (1997). Pericarp browning of postharvest litchi fruit. *Chinese Journal of Tropical Crops*, *18*(2), 53–58. (In Chinese with English abstract).

Zheng, L., Situ, J. J., Zhu, Q. F., Xi, P. G., Zheng, Y., Liu, H. X., & Zhou, X. (2019). Identification of volatile organic compounds for the biocontrol of postharvest litchi fruit pathogen *Peronophythora litchii*. *Postharvest Biology and Technology*, *155*, 37–46. https://doi.org/10.1016/j.foodchem.2005.02.049

Zheng, X., & Tian, S. (2006). Effect of oxalic acid on control of postharvest browning of litchi fruit. *Food Chemistry*, *96*(4), 519–523. https://doi.org/10.1016/j.foodchem.2005.02.049

Zhong, J., Duan, X. W., Qu, H. X., Yang, B., Chen, Y. L., Ruenroengklin, N., & Jiang, Y. M. (2008). Effects of various extraction conditions on phenolic contents and their antioxidant activities of litchi fruit pericarp. *Acta Horticulturae*, *804*, 327–332. https://doi.org/10.17660/ActaHortic.2008.804.46

Zhou, Y., Chen, Z., He, M., Gao, H., Zhu, H., Yun, Z., Qu, H., & Jiang, Y. (2020). Unveiling the complexity of the litchi transcriptome and pericarp browning by single-molecule long-read sequencing. *Postharvest Biology and Technology*, *168*, 111252. https://doi.org/10.1016/j.postharvbio.2020.111252

How to cite this article: Huang, C. C., Paull, R. E., & Wang, T.-T. (2024). Litchi postharvest physiology and handling. *Crop Science*, *64*, 2014–2063. https://doi.org/10.1002/csc2.21274