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Review article

Oxidative metabolism is associated with physiological disorders in fruits stored under multiple environmental stresses

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ABSTRACT

In combination with low temperature, controlled atmosphere storage and 1-methylcyclopropene (ethylene antagonist) application are used to delay senescence of many fruits and vegetables. Controlled atmosphere consists of low O_2 and elevated CO_2. When sub-optimal partial pressures are used, these practices represent multiple abiotic stresses that can promote the development of physiological disorders in pome fruit, including flesh browning and cavities, although there is some evidence for genetic differences in susceptibility. In the absence of surface disorders, fruit with flesh injuries are not easily distinguished from asymptomatic fruit until these are consumed. Oxidative stress metabolites tend to accumulate (*e.g.*, γ-aminobutyrate) or rapidly decline (*e.g.*, ascorbate and glutathione) in vegetative tissues exposed to hypoxic and/or elevated CO_2 environments. Moreover, these phenomena can be associated with altered energy and redox status. Biochemical investigations of *Arabidopsis* and tomato plants with genetically-altered levels of enzymes associated with the γ-aminobutyrate shunt and the ascorbate–glutathione pathway indicate that these metabolic processes are functionally related and critical for dampening the oxidative burst in vegetative and fruit tissues, respectively. Here, we hypothesize that γ-aminobutyrate accumulation, as well energy and antioxidant depletion are associated with the development of physiological injury in pome fruit under multiple environmental stresses. An improved understanding of this relationship could assist in maintaining the quality of stored fruit.

Contents

1. Introduction 143
2. Oxidative stress metabolism 146
 2.1. Energy metabolism during controlled atmosphere storage 146
 2.2. GABA, GHB and pyridine dinucleotides 146
 2.3. Antioxidants 148
 2.4. Ascorbate and glutathione 148
3. Concluding remarks and significance 149
 Acknowledgements 150
 References 150

1. Introduction

Metabolic activity leading to senescence is often minimized to maintain quality and prolong the supply period for fleshy fruits. This is done in storage by using low temperature often in combination with controlled atmosphere (*i.e.*, reduced O_2 and elevated CO_2 partial pressures), which lowers respiration and delays ethylene production and the onset of senescence-related disorders. Low temperature controlled atmosphere storage in commercial operations may be combined with chemical treatments such as 1-methylcyclopropene (1-MCP) to further inhibit ethylene-mediated ripening [1].

Storage recommendations are generally specific to fruit species and their cultivars, as well as geographic location [2]. By contrast, storage under low temperatures and O_2 and CO_2 partial pressures which are not optimal for prolonged duration can lead to the devel-

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Table 1
A summary of select storage-related disorders in pome fruit and their cultivars.

Physiological Disorder	Species/cultivars	Symptoms	Storage parameters	References
Soft scald	*Malus* × *domestica* Borkh. cv. 'Honeycrisp'	Smooth, irregularly shaped soft brown patches with defined edges on peel	0.5–3 °C	[4,5]
Soggy breakdown	*M. domestica* cv. 'Honeycrisp'	Initiates as diffuse browning of cortex, surrounded by barrier of healthy tissue Later, tissue becomes moist and spongy; vasculature undergoes intense browning	0–0.5 °C	[5,6]
Vascular breakdown	*M. domestica* cv. 'Cortland' cv. 'McIntosh'	Browning of vascular bundles which can extend into surrounding cortical tissue	0 °C	[4,7]
Core browning	*M. domestica* cv. 'Cortland' cv. 'McIntosh'	Brown, necrotic flesh around the core	0–3 °C	[4,8]
Senescent breakdown	*M. domestica* cv. 'Cortland' cv. 'McIntosh' cv. 'Macoun'	Brown and soft flesh tissue that initiates underneath peel Largeportions of flesh tissue can become dry	1–3 °C	[4,8,9]
Superficial scald	*M. domestica* cv. 'Granny Smith' cv 'Cortland' cv 'Law Rome' cv. 'Delicious'	Irregular brown patches of peel with no effect on underlying flesh tissue	0–4 °C; some symptoms can occur up to 25 °C	[4,10 and references therein]
	*Pyrus communis*L. cv. 'Bartlett' cv. 'd'Anjou'	Associated with collapse of hypodermal cells culminating in skin browning		
Senescent scald	*P. communis* cv. 'Bartlett'	Dark brown discolouration of the peel, which is associated with aging Fruit remains firm	0–1 °C; can develop following the removal of fruit from storage	[4]
Flesh browning	*M. domestica*	Firm browning of cortical tissues	0.5 °C, 3 kPa O_2, 2 kPa CO_2	[11]
	cv. 'Empire'			
	M. domestica cv. 'Pink Lady'	Brown patches within flesh, which can develop into cavities	0.5 °C, 1.5 kPa O_2, 5 kPa CO_2	[12]
	M. domestica cv. 'Braeburn'	Cortical browning that can be accompanied by lens-shaped cavities In some cases, browning can extend to peel	0.5 °C, 2 kPa O_2, 2-5 kPa CO_2	[13]
Low-O_2 injury	*M. domestica* cv. 'Cox's Orange Pippin' cv. 'McIntosh' cv. 'Delicious'	Areas of peel turn purple or become water soaked and brown, regardless of blush Injury can extend into sub-epidermal region	<1.5 kPa O_2	[4]
Controlled atmosphere-related injury	*M. domestica* cv. 'Honeycrisp'	Irregular browning of cortex, which can be associated with lens-shaped cavities	3 °C, 1–4.5 kPa O_2, 0.5–3 kPa CO_2; can occur to a small extent at 21 kPa O_2	[14,15]
Internal CO_2 injury (also known as brown heart)	*M. domestica* cv. 'Fuji'	Dark brown flesh that can be accompanied by cavities	0.5 °C, 0.5 kPa O_2, 3 kPa CO_2	[16,17 and references therein]
	P. communis cv. 'Conference'	Brown cortical tissue and/or cortical cavities	−0.5 °C, 2 kPa O_2, 5 kPa CO_2	
Core break-down/internal break-down/internal browning	*P. communis* cv. 'Conference' cv. 'Bartlett'	Initiates as water soaked and brown core tissue, followed by browning and cavitation within surrounding tissues	0.5–3 kPa O_2 with or without 10 kPa CO_2	[4,17 and references therein,18]
External CO_2 injury	*M. domestica* cv. 'Empire' cv. 'McIntosh'	Rough, brown uneven sunken lesions of the peel	2–2.5 kPa O_2, 2–5 kPa CO_2; can be exacerbated by 1-MCP	[19,20]

opment of physiological disorders in temperate fruits ([3]; Table 1), including two of the most highly cultivated tree fruits in the world, apple (*Malus* × *domestica* Borkh.) and European pear (*Pyrus communis* L.) (Food and Agriculture Organization of the United Nations: Statistics, FAOSTAT 2012). Visible symptoms of a select number of physiological disorders associated with storage under these multiple environmental stresses are summarized in Table 1, including for new germplasm (*i.e.*, 'Honeycrisp' apples) for which no consistent controlled atmosphere storage recommendations exist. The predominant chilling injuries in apple fruit include core browning,