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‘Honeycrisp’ Apple (*Malus domestica* Borkh.) Fruit Response to Controlled Atmosphere Storage with the Low Oxygen Limit Established by Monitoring Chlorophyll Fluorescence

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***Abstract*. Postharvest management of apple fruit ripening using controlled atmosphere (CA) storage can be enhanced because CA oxygen concentration is decreased to close to the anaerobic compensation point (ACP). Monitoring fruit chlorophyll fluorescence (CF) is a technology to assess fruit response to low pO_2 as fluorescence increases as pO_2 reaches a critically low concentration. This type of pO_2 management has been referred to as dynamic atmosphere storage (DCA). Use of very low pO_2 can enhance post-storage apple fruit quality for many cultivars, allowing better firmness retention and prevention of superficial scald, compared with fruit stored at higher pO_2 during CA. ‘Honeycrisp’ is a chilling-sensitive cultivar with little risk of firmness loss or superficial scald during storage; however, other aspects of fruit-quality loss during storage, including soluble solids content (SSC), titratable acidity (TA), peel greasiness, and physiological disorder development may be impacted by pO_2. A 2-year study was conducted to identify ‘Honeycrisp’ fruit-quality impacts of CA storage with a low-pO_2 setpoint determined by using CF. ‘Honeycrisp’ apples were held 7 days at 10 °C after harvest, then at 3 °C. An additional treatment with 1-methylcyclopropene (1-MCP) was conducted in year two. CA was established 48 hours after transfer to 3 °C. In both years, fruit CF increased when pO_2 decreased to ≈0.3 kPa O_2 and then decreased after pO_2 was increased to 0.5 kPa. Additional CA pO_2 concentrations above 0.3 kPa were also maintained for other fruit. Fruit internal disorder incidence increased as pO_2 decreased and with 1-MCP use. Changes in SSC, TA, and peel yellowing were inconsistently reduced by storage at lower pO_2. Peel greasiness did not develop in either year. CA did not impact the incidence of chilling disorders regardless of pO_2. Results indicate some aspects of ‘Honeycrisp’ fruit quality can be enhanced as CA pO_2 decreases; however, pO_2 above the low pO_2 threshold did not prevent internal physiological disorder development.**

‘Honeycrisp’ apple exhibits little loss of firmness over an extended cold storage period in air or CA (Tong et al., 1999; Watkins and Nock, 2012). Other aspects of ripening progress during storage, including loss of titratable acidity and soluble solids content, include development of peel greasiness, peel yellowing, and senescent disorders (Watkins et al., 2004, 2005). ‘Honeycrisp’ is susceptible to the chilling disorders soft scald and soggy breakdown (Tong et al., 2003), but the risk can be managed by a conditioning period at 10 to 20 °C after harvest, before storage at a lower temperature (Contreras et al., 2014; DeLong et al., 2004a; Watkins et al., 2004). CA storage of ‘Honeycrisp’ can induce internal browning (Contreras et al., 2014; DeEll et al., 2015, 2016), but CA also has the practical use of extending fruit storage life if ripening can be slowed and fruit quality preserved in the absence of physiological disorders (Watkins and Nock, 2012).

Fruit chlorophyll fluorescence is a means to detect low-pO_2 stress in apple fruit (DeEll et al., 1999) and to identify the low-pO_2 limit (LOL) for apple fruit during CA storage, a type of dynamic CA (DCA) storage management (DeLong et al., 2004b). Apples stored at a pO_2 slightly above the LOL can have enhanced preservation of firmness and titratable acidity (DeLong et al., 2004b; Zanella et al., 2005), as well as reduced incidence of superficial scald (Zanella, 2003), compared with storage in higher pO_2 during CA. Storage of apples at pO_2 close to the LOL has been suggested to provide a nonchemical means for physiological disorder control, particularly for superficial scald in organic fruit, for which synthetic postharvest chemicals is prohibited (DeLong et al., 2007).

CA storage of ‘Honeycrisp’ has not consistently been observed to enhance post-storage fruit quality compared with air storage (Contreras et al., 2014; DeEll et al., 2015, 2016; El-Shiekh et al., 2002; Mattheis et al., 2017; Serban et al., 2019; Watkins and Nock, 2012). However, these studies were conducted using pO_2 setpoints above 1 kPa. How ‘Honeycrisp’ CA storage at pO_2 less than 1 impacts fruit quality attributes other than firmness (DeLong et al., 2004a) has not been reported.

The objective of this research was to evaluate ‘Honeycrisp’ apple response to CA storage under a range of low pO_2, with the lowest setpoint determined based on fruit CF.

Materials and Methods

Plant material and cold storage procedures. ‘Honeycrisp’ (*Malus ×domestica* Borkh.) apples from a commercial orchard in central Washington State were used in two consecutive seasons. Apples determined by the grower to be horticulturally mature were obtained the day of harvest. Fruit without external defects were placed on pressed-fiber trays, and then these trays were put into cardboard boxes (control fruit), or in year two were placed into an 800-L gas-tight metal cabinet for 1-MCP treatment. The 1-MCP treatment was conducted in a cold room separate from that in which control fruit were held; both cold rooms were maintained at 10 °C. Fruit on trays in the metal tank were exposed to 42 $\mu mol \cdot L^{-1}$ 1-MCP (AgroFresh, Inc., Spring House, PA) for 24 h, then the trays were removed from the metal tank, placed into cardboard boxes, and moved to the same cold room as the controls. The controls and 1-MCP-treated fruit were held for 7 d at 10 °C, then they were moved to a cold room held at 3 °C for the remainder of the storage period. Fruit stored in air remained packed in cardboard boxes, while fruit for CA were removed from boxes and stored on trays in sealed, 0.14-m^3 CA chambers. Two CA chambers were used to monitor apple chlorophyll fluorescence using the HarvestWatch system (Satlantic Inc., Halifax, N.S., Canada). CA was generated and maintained as described previously (Mattheis et al., 2017). After 2 d at 3 °C, 1.5 and 2.0 kPa O_2 were established in years one and two, respectively, with pCO_2 at 0.5 kPa in both years. After 2 additional days, pO_2 was reduced in the two chambers with the CF monitoring system until an increase in CF occurred. The pO_2 at which the CF increase occurred was identified as the LOL. Following the identification of the LOL, pO_2 settings

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for additional CA chambers containing sample fruit were set in year one at the LOL: LOL + 0.2 kPa; LOL + 0.5 kPa; and 1.5 kPa. In year two, pO_2 setpoints were the following: LOL + 0.2 kPa; 1.0 kPa and 2.0 kPa. In both years, additional fruit at pO_2 set at the LOL + 0.2 kPa were monitored using the HarvestWatch system. The CA system was operated using commercial controls (Empire Controls, Chelan, WA) as described previously by Mattheis et al. (2017). Storage duration was 4 and 8 months in both years. When CA chambers were resealed after removing fruit after 4 months, chambers were purged with N_2 and CO_2 sufficient to reestablish the kPO_2 and kCO_2 setpoints within 1 h.

Fruit quality assessment. Fruit were assessed at harvest as well as the day of and 7 d after removal from cold storage. Post-cold storage temperature was 20 °C. All fruit evaluation procedures were as described previously by Mattheis et al. (2017).

Experimental design and statistical analysis. Experiments were conducted with a completely randomized design, with 3 replicates of 6 individual fruit (starch, internal ethylene concentration, firmness, peel ground color); 9 replicates prepared with 2 fruit (soluble solids content and titratable acidity); 4 replicates containing 4 fruit (ethylene production); 6 replicates of 12 fruit for physiological disorders, for each storage atmosphere/storage duration combination. Statistical analyses were conducted with SAS 9.4 (SAS Institute, Raleigh, NC). Disorder incidence was arcsine square root transformed before analysis. Significant treatment differences for fruit quality attributes and storage disorders were identified using analysis of variance and treatment means separated using Tukey's honestly significant difference. Maturity at harvest results by year were compared using the SAS *t* test procedure.

Results

At harvest, values for starch index, peel ground color, and SSC were higher, titratable acidity lower, and internal ethylene concentration (IEC) and firmness similar for year one compared with year two (Table 1). The LOL was 0.3 kPa in both years. Based on these results, in year one the lowest pO_2 concentrations were at the LOL of 0.3 kPa O_2 and 0.5 kPa. In year two, the lowest pO_2 was 0.2 kPa higher than the LOL, 0.5 kPa. During the storage period in both years, CF of fruit held at 0.5 kPa did not exhibit an abrupt increase as had been observed during determination of the LOL.

Incidence of soft scald in both years was low, and there was no soggy breakdown in year one (Tables 2 and 3). In year one there were no storage treatment effects on soft scald after 4 months, and the disorder was present only on fruit stored at 0.3 and 0.5 kPa O_2 at 8 months. No treatment effects on soft scald and soggy breakdown were present in year two. Internal browning incidence increased as storage pO_2 decreased in both years and with 1-MCP treatment in year two—although the symptoms differed between years (radial browning in year one, diffuse browning in year two). Cortex cavities, calyx-end peel browning, and core flush developed only in year two, with calyx-end leather blotch highest in fruit treated with 1-MCP and stored at 0.5 kPa O_2. Core flush only developed in 1-MCP fruit stored in air. The incidence of nonchilling disorders increased as pO_2 decreased, in both years.

Peel background color ratings were lower (greener) as pO_2 decreased and for 1-MCP–treated fruit stored in air. Control fruit stored in air had the highest peel color (yellow) rating. The pO_2 influenced SSC and TA in both years, with fruit stored in air having the lowest values. In year one after 8 months, TA retention increased as pO_2 decreased; while in year two, an atmosphere × 1-MCP interaction influenced TA values. Within some but not all pO_2 treatments, TA was higher for 1-MCP fruit. There were no pO_2 or 1-MCP treatment effects on firmness. IEC was highest in air-stored fruit in both years (controls in year two). Ethylene production was influenced by an atmosphere × 1-MCP interaction in year two at both 4 and 8 months.

Discussion

As 'Honeycrisp' loses little if any firmness during storage (Tong et al., 1999; Wargo and Watkins, 2004) and has not been reported to be susceptible to superficial scald, the benefit of CA storage resides in retention of other aspects of fruit quality and limiting disorder development (DeEll et al., 2015; DeLong et al., 2006; Mattheis et al., 2017; Watkins and Nock, 2012). While the results herein show CA storage reduces SSC and TA loss and development of peel yellow color compared with fruit stored in air, increased incidence of soft scald in one year and nonchilling disorders in both years as pO_2 setpoint decreased reduces the potential use for CA at and near the LOL. These results are consistent with responses in 'Anjou' pear fruit, where internal browning developed when pO_2 was held at 0.2 kPa above the LOL (Mattheis and Rudell, 2011; Mattheis et al., 2013). While increased internal browning risk has been observed in other apple cultivars as pO_2 decreases (Watkins and Mattheis, 2019), soft scald risk has not been reported to have a similar relationship. As the relationship between soft scald and pO_2 was observed in only one of the two years and incidence was relatively low, more research is needed to conclusively establish that pO_2 can influence soft scald development.

While the range of pO_2 values in the two seasons were different, internal browning injury increased in both years as pO_2 decreased. The lowest pO_2 in the first year was at the LOL where a high % of internal browning occurred; but internal browning also occurred at 0.5 kPa O_2, 0.2 kPa above the measured LOL in both years, indicating that a risk for internal browning exists even above the LOL. The highest pO_2 in year two, 2 kPa, was above that of year one to attempt to avoid (unsuccessfully) internal browning that had occurred at the highest pO_2 in year one, 1.5 kPa. Development of nonchilling disorders in fruit stored at the highest pO_2 in both years, compared with no injury in fruit stored in air, is consistent with a risk of disorder development even at relatively high pO_2 (Contreras et al., 2014; Watkins and Nock, 2012).

The pre-CA storage conditioning protocol can impact 'Honeycrisp' physiological disorder risk with conditioning temperature (Contreras et al., 2014) and duration (DeEll et al., 2016), both factors influencing CA injury. The conditioning protocol used here, 10 °C for 7 d, is not optimum for CA disorder avoidance based on that previous work. Whether use of higher conditioning temperature and/or longer duration would reduce disorder risk at low pO_2 is unknown—as is how higher temp/longer duration conditioning would influence the low pO_2 impacts on fruit quality, particularly SSC, TA, and peel color. Longer conditioning duration can enhance lenticel breakdown, bitter pit/blotch, and peel greasiness (DeEll et al., 2016).

Higher disorder incidence in 1-MCP–treated fruit stored in CA is consistent with previous reports (DeEll et al., 2015, Lum et al., 2016). Higher internal browning in 1-MCP–treated fruit compared with control fruit stored only at 0.5 and 1.0 pO_2 may indicate fruit in this study had a lower susceptibility to this disorder compared with that used by Lum et al. (2016), and that injury occurred only when fruit were stored in the

Table 1. 'Honeycrisp' fruit maturity at harvest and the low oxygen limit (LOL) in 2 consecutive years. Values are means; n = 3 replicates of 6 fruit for internal ethylene concentration (IEC), starch index (Starch: 1 = full starch, 6 = clear), firmness, and peel ground color (1 = green, 5 = yellow); n = 9 replications of 2 fruit for titratable acidity (TA) and soluble solids content (SSC); and n = 2 for LOL. LOL was determined using the HarvestWatch system. Mean comparison by Student's *t* test.

Yr	IEC ($mmol{\cdot}m^{-3}$)	Starch (1–6)	Firmness (N)	Peel color (1–5)	SSC (%)	TA (%)	LOL (kPa O_2)
1	0.94	6.0	69.9	3.8	0.500	13.5	0.3
2	0.71	5.5	67.2	2.9	0.589	13.1	0.3
	NS	*	NS	***	*	*	NS

NS, *, ***Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Table 2. 'Honeycrisp' fruit quality and physiological disorders after storage, year one. Fruit were held 7 d at 10 °C after harvest then at 3 °C in air or a CA with 0.3 to 1.5 kPa O_2 with 0.5 kPa CO_2 for 4 or 8 mo. Apples were held 7 d at 20 °C after removal from cold storage. Values are means; n = 6 replicates of 12 fruit for soft scald (SS) and radial internal browning (RIB); n = 3 replicates of 6 fruit for peel ground color (PGC) and firmness (Firm); n = 9 replicates of 2 fruit for soluble solids content (SSC) and titratable acidity (TA); and n = 4 replicates of 4 fruit for ethylene production (C_2H_4). Means within columns within months followed by different letters are significantly different according to Tukey's honestly significant difference.

Months	O_2 (kPa)	SS (%)	RIB (%)	PGC (1–5)	Firm (N)	SSC (%)	TA (%)	C_2H_4 (ηmol·g^{-1}·s^{-1})
4	Air	0 NS	0 NS	4.9 a	66.8	12.0 c	0.314 c	0.57 a
	1.5	3	6	4.2 b	66.2	12.2 bc	0.358 b	0.28 b
	0.8	0	11	4.3 b	69.0	12.9 a	0.413 a	0.31 b
	0.5	3	3	4.3 b	65.5	12.7 ab	0.346 bc	0.34 b
	0.3	0	3	4.4 b	62.8	12.5 abc	0.346 bc	0.31 b
		NS	NS	**	NS	**	***	***
8	Air	0 b	0 c	5.0 a	61.2	11.4 c	0.249 d	0.91 a
	1.5	0 b	6 bc	5.0 a	66.5	11.6 c	0.325 c	0.34 c
	0.8	0 b	19 ab	5.0 a	64.2	12.5 b	0.350 bc	0.48 b
	0.5	8 a	33 a	5.0 a	65.9	13.1 a	0.380 ab	0.34 c
	0.3	6 ab	31 a	4.0 b	66.1	12.7 ab	0.387 a	0.25 c
		*	**	**	NS	***	***	***

NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 3. 'Honeycrisp' fruit quality and physiological disorders after storage, year two. Fruit were held 7 d at 10 °C after harvest, then at 3 °C in air or a CA with 0.3 to 1.5 kPa O_2 with 0.5 kPa CO_2. Apples were held 7 d at 20 °C after removal from cold storage. Values are means; n = 6 replicates of 12 fruit for soft scald (SS), soggy breakdown (SB), diffuse internal browning (DIB), cavities (Cav), calyx-end leather blotch (CLB), core flush (CF), and total nonchilling disorders (TNC); n = 3 replicates of 6 fruit for peel ground color (PGC) and firmness (Firm); n = 9 replicates of 2 fruit for soluble solids content (SSC) and titratable acidity (TA); and n = 4 replicates of 4 fruit for ethylene production (C_2H_4). Means within columns within month followed by different letters are significantly different according to Tukey's honestly significant difference.

Months	1-MCP	O_2 (kPa)	SS (%)	SB (%)	DIB (%)	Cav (%)	CLB (%)	CF (%)	TNC (%)	PGC (1–5)	Firm (N)	SSC (%)	TA (%)	C_2H_4 (ηmol·g^{-1}·s^{-1})
4	Control	Air	1	3	0 c	0	0 b	0	0 c	4.7 a	63.6	12.9	0.391 d	0.65 a
	1-MCP		0	0	0 c	6	3 b	0	9 bc	3.6 bc	64.1	13.4	0.472 ab	0.08 c
	Control	2.0	3	3	3 bc	0	0 b	0	3 bc	3.4 bc	65.0	13.3	0.427 c	0.42 b
	1-MCP		0	0	0 c	0	0 b	0	0 c	3.8 b	61.8	13.2	0.446 bc	0.02 d
	Control	1.0	0	0	6 bc	0	3 b	0	6 bc	3.6 bc	65.3	13.1	0.442 bc	0.37 b
	1-MCP		0	0	22 ab	0	3 b	0	22 ab	3.7 b	64.8	13.5	0.467 ab	0.02 cd
	Control	0.5	0	0	12 bc	0	6 b	0	12 bc	3.3 c	64.5	13.5	0.449 bc	0.40 b
	1-MCP		3	0	36 a	3	19 a	0	36 a	3.7 bc	63.3	13.6	0.490 a	0.01 d
			NS	NS	A×M **	NS	A×M ***	NS	A×M *	A×M ***	NS	A** M*	A×M ***	A×M **
8	Control	Air	0	0	0 d	0	0 b	0 b	0	5.0 a	65.4	12.9	0.360 d	0.74 a
	1-MCP		6	0	0 d	0	0 b	9 a	9	4.0 b	64.8	13.0	0.461 a	0.13 e
	Control	2.0	0	0	8 c	6	0 b	0 b	14	3.4 cde	64.0	13.0	0.419 c	0.40 b
	1-MCP		3	0	3 cd	3	0 b	0 b	6	3.1 e	62.9	13.3	0.423 bc	0.01 f
	Control	1.0	0	0	9 c	6	0 b	0 b	9	3.5 cd	61.0	13.2	0.411 c	0.25 d
	1-MCP		3	0	24 b	0	17 a	0 b	21	3.7 bc	63.7	13.3	0.439 b	0.01 f
	Control	0.5	0	0	17 bc	3	22 a	0 b	28	3.3 de	64.5	13.1	0.426 bc	0.31 c
	1-MCP		1	0	37 a	3	21 a	0 b	37	3.5 cd	62.8	13.7	0.460 a	0.01 f
			NS	NS	A×M **	NS	A×M ***	A×M *	A***	A×M ***	NS	A*** M***	A×M ***	A×M ***

A = atmosphere; M = 1-MCP; A×M = atmosphere × 1-MCP interaction.
NS, *, **, ***Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

low-pO_2 atmospheres that induced more stress compared with that at higher pO_2.

CA-stored 'Honeycrisp' with or without previous 1-MCP treatment can have higher SSC and TA compared with controls stored in air (DeEll et al., 2015). Fruit with higher TA received higher sensory scores for acid taste in the same study. Impacts of CA with or without 1-MCP on other sensory components indicates additional impacts of these storage technologies on post-storage fruit quality. Control fruit stored in air in this study always had the lowest TA, illustrating the value of CA and/or 1-MCP for preserving this quality attribute for consumers preferring acid taste. However, the lack of consistently higher TA values accompanying decreased CA pO_2 questions the need for very low pO_2 for 'Honeycrisp'. What, if any, impact pO_2 has on 'Honeycrisp' peel greasiness development is undetermined, because greasiness did not develop in either year of the study.

Factors contributing to the difference in internal browning symptoms in the 2 years of this study are unknown. Research with 'Gala' apple has shown storage temperature and 1-MCP treatment can impact internal browning symptom development (Lee et al., 2016). As the postharvest temperature protocol used in both years in this study was identical, and internal browning symptoms in year two when 1-MCP was used were identical in control and treated fruit, other factors, perhaps preharvest conditions (Lachapelle et al., 2013, 2017; Tong et al., 2016), may have contributed to the difference between years. Core browning in year two in fruit stored in air but only in 1-MCP–treated fruit is consistent with results reported by Serban et al. (2019) but contrasts a previous report (Watkins and Nock, 2012) where the disorder was present in fruit stored in CA and incidence was lowest in 1-MCP–treated fruit.

Symptoms of the calyx-end peel injury detected in this study were consistent with 'Honeycrisp' peel leather blotch reported previously (DeEll et al., 2016; Mattheis et al., 2017; Serban et al., 2019). Thus pCO_2 (Anderson, 1967) and 1-MCP treatment (DeEll et al., 2015) both influence development of peel CO_2 injury, the symptoms of which are consistent with what was observed here, and increased incidence with decreased O_2 kPa may indicate increased CO_2 sensitivity as storage O_2 kPa decreases or may show that the disorder is a form of low-oxygen injury.

The low-oxygen threshold identified by monitoring CF in both years was 0.1 kPa less than that reported previously for 'Honeycrisp' (DeLong et al., 2004b; Wright et al., 2010). Use of a range of pO_2 above the threshold revealed a relationship between pO_2 and internal browning that developed at pO_2 well above the threshold value. As most of the fruit evaluated after storage was not subject to the initial low-pO_2

regime used to establish the low-O_2 threshold, internal browning could not have resulted from a relatively brief low-O_2 exposure at the threshold value. Development of injury in this study, compared with the lack of injury in previously reported work (DeLong et al., 2004b), may reflect seasonal, climatic, orchard, or other factors that can influence apple fruit disorder development (Watkins and Mattheis, 2019). The absence of an abrupt change in CF during the storage period after pO_2 had been increased to 0.5 kPa O_2, 0.2 kPa above the threshold value, indicates the metabolic events resulting in internal browning in this study did not result in a change in CF typical for establishing the low-O_2 threshold.

Postharvest management of 'Honeycrisp' largely focuses on disorder avoidance, both CI- and CA-related internal browning. Benefits of CA to fruit-quality maintenance reside outside of firmness and can be obtained at pO_2 well above the CF low-O_2 threshold. Considering the risk of internal browning based on this study's results, CA at pO_2 values well above the low-O_2 threshold (as determined here using chlorophyll fluorescence) provides fruit-quality benefits with a relatively low risk of CA-induced internal disorders, compared with fruit stored in air.

Literature Cited

Anderson, R.E. 1967. Experimental storage of eastern-grown 'Delicious' apples in various controlled atmospheres. Proc. Amer. Soc. Hort. Sci. 91:810–820.

Contreras, C.N., N. Alsmairat, and R. Beaudry. 2014. Prestorage conditioning and diphenylamine improve resistance to controlled-atmosphere-related injury in 'Honeycrisp' apples. HortScience 49:76–81, doi: 10.21273/HORTSCI.49.1.76.

DeEll, J.R., O. van Kooten, R.K. Prange, and D.P. Murr. 1999. Applications of chlorophyll fluorescence techniques in post-harvest physiology. Hort. Rev. 23:69–107.

DeEll, J.R., B. Ehsani-Moghaddam, A.J. Bowen, and I. Lesschaeve. 2015. Effects of 1-methycyclopropene and controlled atmosphere storage on the quality of 'Honeycrisp' apples. Acta Hort. 1071:483–488, doi: 10.17660/ActaHortic.2015.1071.62.

DeEll, J.R., G.G. Lum, and B. Ehsani-Moghaddam. 2016. Effects of delayed controlled atmosphere storage on disorder development in 'Honeycrisp' apples. Can. J. Plant Sci. 96:621–629, doi: 10.1139/cjps-2016-0031.

DeLong, J.M., R.K. Prange, and P.A. Harrison. 2004a. The influence of pre-storage delayed cooling on quality and disorder incidence in 'Honeycrisp' apple fruit. Postharvest Biol. Technol. 34:353–358, doi: 10.1016/j.postharvbio.2004.10.001.

DeLong, J.M., R.K. Prange, J.C. Leyte, and P.A. Harrison. 2004b. A new technology that determines low-oxygen thresholds in controlled-atmosphere-stored apples. HortTechnology 14:262–266, doi: 10.21273/HORTTECH.14.2.0262.

DeLong, J.M., R.K. Prange, P.A. Harrison, C.G. Embree, D.S. Nichols, and H.A. Wright. 2006. The influence of crop-load, delayed cooling and storage atmosphere on post-storage quality of 'Honeycrisp' apples. J. Hort. Sci. Biotechnol. 81:391–396, doi: 10.1080/14620316.2006.11512078.

DeLong, J.M., R.K. Prange, and P.A. Harrison. 2007. Chlorophyll fluorescence based low O_2 storage of organic 'Cortland' and 'Delicious' apples. Acta Hort. 737:31–37, doi: 10.17660/ActaHortic.2007.737.3.

El-Shiekh, A.F., C.B.S. Tong, J.J. Luby, E.E. Hoover, and D.S. Bedford. 2002. Storage potential of cold-hardy apple cultivars. J. Amer. Pomol. Soc. 56:34–45.

Lachapelle, M., G. Bourgeois, J. DeEll, K.A. Stewart, and P. Séguin. 2013. Modeling the effect of preharvest weather conditions on the incidence of soft scald in 'Honeycrisp' apples. Postharvest Biol. Tech. 85:57–66, doi: 10.1016/j.postharvbio.2013.04.004.

Lachapelle, M., G. Bourgeois, J. DeEll, K.A. Stewart, and P. Séguin. 2017. Modeling the effect of preharvest weather conditions on the incidence of soggy breakdown in 'Honeycrisp' apples. HortScience 52:756–763, doi: 10.21273/HORTSCI10761-16.

Lee, J., J.P. Mattheis, and D.R. Rudell. 2016. Storage temperature and 1-methylcyclopropene treatment affect storage disorders and physiological attributes of 'Royal Gala' apples. HortScience 51:84–93, doi: 10.21273/HORTSCI.51.1.84.

Lum, G.B., C.J. Brikis, K.L. Deyman, S. Subedi, J.R. DeEll, B.J. Shelp, and G.G. Bozzo. 2016. Pre-storage conditioning ameliorates the negative impact of 1-methylcyclopropene on physiological injury and modifies the response of antioxidants and γ-aminobutyrate in 'Honeycrisp' apples exposed to controlled-atmosphere conditions. Postharvest Biol. Technol. 116:115–128, doi: 10.1016/j.postharvbio.2016.01.013.

Mattheis, J.P., D.R. Rudell, and I. Hanrahan. 2017. Impacts of 1-methylcyclopropene and controlled atmosphere established during conditioning on development of bitter pit in 'Honeycrisp' apples. HortScience 52:132–137, doi: 10.21273/HORTSCI11368-16.

Mattheis, J.P. and D. Rudell. 2011. Responses of 'd'Anjou' pear (*Pyrus communis* L.) fruit to storage at low oxygen set-points determined by monitoring fruit chlorophyll fluorescence. Postharvest Biol. Technol. 60:125–129, doi: 10.1016/j.postharvbio.2010.12.007.

Mattheis, J., D. Felicetti, and D.R. Rudell. 2013. Pithy brown core in 'd'Anjou' pear (*Pyrus communis* L.) fruit developing during controlled atmosphere storage at pO_2 determined by monitoring chlorophyll fluorescence. Postharvest Biol. Technol. 86:259–264, doi: 10.1016/j.postharvbio.2013.07.006.

Serban, C., L. Kalcsits, J. DeEll, and J.P. Mattheis. 2019. Responses of 'Honeycrisp' apples to short-term controlled atmosphere storage established during temperature conditioning. HortScience 54:1532–1539, doi: 10.21273/HORTSCI14182-19.

Tong, C., D. Kruger, Z. Vickers, D. Bedford, J. Luby, A. El-Shiekh, K. Shackel, and H. Ahmadi. 1999. Comparison of softening-related changes during storage of 'Honeycrisp' apple, its parents, and 'Delicious'. J. Amer. Soc. Hort. Sci. 124:407–415, doi: 10.21273/JASHS.124.4.407.

Tong, C.B.S., D.S. Bedford, J.J. Luby, F.M. Propsom, R.M. Beaudry, J.P. Mattheis, C.B. Watkins, and S.A. Weis. 2003. Location and temperature effects on soft scald in 'Honeycrisp' apples. HortScience 38:1153–1155, doi: 10.21273/HORTSCI.38.6.1153.

Tong, C.B.S., H.-Y. Chang, J.K. Boldt, Y.B. Ma, J.R. DeEll, R.E. Moran, G. Bourgeois, and D. Plouffe. 2016. Diffuse flesh browning in 'Honeycrisp' apple fruit is associated with low temperatures during fruit growth. HortScience 51:1256–1264, doi: 10.21273/HORTSCI11179-16.

Wargo, J.M. and C.B. Watkins. 2004. Maturity and storage quality of 'Honeycrisp' apples. HortTechnology 14:496–499, doi: 10.21273/HORTTECH.14.4.0496.

Watkins, C.B., J.F. Nock, S.A. Weis, S. Jayanty, and R.M. Beaudry. 2004. Storage temperature, diphenylamine, and pre-storage delay effects on soft scald, sorry breakdown and bitter pit of 'Honeycrisp' apples. Postharvest Biol. Technol. 32:213–221, doi: 10.1016/j.postharvbio.2003.11.003.

Watkins, C.B., M. Erkan, J.F. Nock, K.A. Iungerman, R.M. Beaudry, and R.E. Moran. 2005. Harvest date effects on maturity, quality, and storage disorders of 'Honeycrisp' apples. HortScience 40:164–169, doi: 10.21273/HORTSCI.40.1.164.

Watkins, C.B. and J.F. Nock. 2012. Controlled-atmosphere storage of 'Honeycrisp' apples. HortScience 47:886–892, doi: 10.21273/HORTSCI.47.7.886.

Watkins, C.B. and J.P. Mattheis. 2019. Apple, p. 165–206. In: S. Tonetto de Freitas and S. Pareek (eds.). Postharvest physiological disorders in fruits and vegetables. CRC Press, Boca Raton, FL, doi: 10.1201/b22001.

Wright, H., J. DeLong, P.A. Harrison, A.H.L.A.N. Gunawardena, and R.K. Prange. 2010. The effect of temperature and other factors on chlorophyll *a* fluorescence and the lower oxygen limit in apples (*Malus domestica*). Postharvest Biol. Technol. 55:21–28, doi: 10.1016/j.postharvbio.2009.07.011.

Zanella, A. 2003. Control of apple superficial scald and ripening—A comparison between 1-methycyclopropene and diphenylamine postharvest treatments, initial low oxygen stress and ultra-low oxygen storage. Postharvest Biol. Technol. 27:69–78, doi: 10.1016/S0925-5214(02)00187-4.

Zanella, A., P. Cazzanelli, A. Panarese, M. Coser, M. Cecchinel, and O. Rossi. 2005. Fruit fluorescence response to low oxygen stress: Modern storage technologies compared to 1-MCP treatment of apple. Acta Hort. 682:1535–1542, doi: 10.17660/ActaHortic.2005.682.204.