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Nasim Kheshti
Chapman University, khesh100@mail.chapman.edu

Anderson Adriano Martins Melo
Chapman University, melo@chapman.edu

Alan Baquero Cedeno
Chapman University

David Obenland
United States Department of Agriculture

Anuradha Prakash
Chapman University, prakash@chapman.edu

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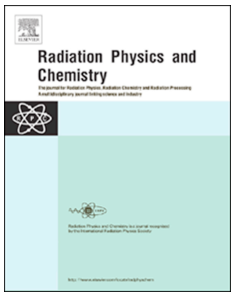

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Physiological response of 'Fuji' apples to irradiation and the effect on quality

Nasim Kheshti[a], Anderson Adriano Martins Melo[a,*], Alan Baquero Cedeno[a], David Obenland[b], Anuradha Prakash[a]

[a]Chapman University, Food Science Department, One University Drive, Orange CA 92866, USA.

[b]USDA, Agricultural Research Service, San Joaquin Valley Agricultural Sciences Center, 9611 South Riverbend Avenue, Parlier CA 93648-9757, USA

E-mail addresses: n.kheshti@gmail.com (N. Kheshti), anderson.melo@ufv.br (A. A. M. Melo, [*]Corresponding author), alan_2988@live.com (A. B. Cedeno), david.obenland@ars.usda.gov (D. Obenland), prakash@chapman.edu (A. Prakash)

ABSTRACT

The objective of this study was to determine the influence of irradiation-induced physiological responses on quality parameters in 'Fuji' apples. Apples were treated at 377 and 1148 Gy, stored for 7 days at 1˚C to mimic ground transportation to Mexico and another 7 days at ambient temperature to simulate retail and consumer storage conditions. Irradiation suppressed ethylene production, especially in the 1148 Gy treated apples, which was consistent with lower activities of 1-aminocyclopropane-1-carboxylate oxidase (ACO). A dose-dependent increase in respiration rate corresponded with decreases in titratable acidity (TA) and organic acids. Higher electrolyte leakage in apples irradiated at the 1148 Gy dose was not related to Malondialdehyde (MDA) content, which was unaffected by irradiation. Irradiation lessened aroma volatile content

at 1148 Gy but there was much lesser affect at the 377 Gy dose. Loss of firmness was the only major quality attribute impacted, but consumers could not tell the difference between control and apples treated at 377 Gy in terms of flavor and visual quality. Irradiation at doses 377 Gy or lower could be used as an alternative to conventional phytosanitary treatments for Fuji apples destined to Mexico.

Keywords: Ethylene; ACC oxidase; respiration rate; e-beam; volatile compounds.

1. INTRODUCTION

In 2016, irradiation was approved as a phytosanitary treatment for apples exported from California to Mexico, following a request by the California Apple Commission (PExD, 2018; CA Apple Commission, 2017). Irradiation has been used for phytosanitary treatment of other fruit such as mangoes, dragon fruit, rambutan, and guava for over two decades, and since 2000 the global commercial use of irradiation for fruit and vegetables has increased about 10% annually (Hallman and Blackburn, 2016).

The desired effect of irradiation to inactivate insects is a function of the direct impact on DNA and RNA molecules or indirectly through the random action of water radiolytic products and generated reactive oxygen species (ROS) on structural and functional cellular components such as cell membranes, which together lead to sterility, morbidity or mortality (Smith and Pillai, 2004; Jeong and Jeong, 2018). These effects of ionizing irradiation can also impact fruit cellular structure and physiology. In apples irradiation reduces ethylene production (Fan and Mattheis, 2001; Fan et al., 2001) and stimulates respiration rate (Massey Jr et al., 1964).

Apples depend strongly on climacteric ethylene to ripen, and treatments that suppress ethylene production or perception delay ripening (Fan et al. 1999), influencing quality parameters such as texture, aroma and flavor. Production of volatile compounds and changes in texture are under direct control of ethylene through its role on regulating gene expression of enzymes responsible for changes in fruit quality associated with ripening (Yang et al., 2016; Ireland et al. 2014).

Ethylene synthesis is reliant on the activity of 1-aminocyclopropane-1-carboxylate oxidase (ACO), which catalyzes the last step in ethylene biosynthesis (Ruduś et al. 2013). In irradiated tomatoes at the pre-climacteric stage, a decrease in the ACO activity has been correlated with membrane damage (Larrigaudière et al. 1990). In apples, however, the effect of irradiation on ACO activity is not known.

Irradiation has been shown to damage the structure of the cell walls (Kovacs et al., 1988) and affect the functionality of membranes through inhibition of H^+-ATPase (Dong et al., 1994). Thus, we believe that reduced ethylene production in irradiated apples may be a function of damage to the cell membrane and reduced ACO activity. While previous studies have evaluated the effect of irradiation on apple quality (Drake et al., 1999, Al-Bachir, 1999) and documented suppression of ethylene, Fan et al., 2001), the causes of ethylene suppression and their relation to membrane damage have not been explored in apples. Mexico is a major export market for fresh California apples (CA Apple Commission, 2017). Mexico requires apples from California to be held at cold temperatures (0˚C for 40 days or at 3.3 ˚C for 90 days) or fumigated with methyl bromide to prevent spread of insect pests such as the light brown apple moth (*Epiphyas postvittana*) and the Oriental fruit moth (*Grapholita molesta*) (PExD, 2018). Fumigation

is the common phytosanitary treatment for California apples sent to Mexico, but methyl bromide is an ozone-depleting chemical and it is in the process of being phased out (EPA 2018). Also, 'Fuji' is among the varieties sensitive to fumigation which causes internal browning, scald and stain. The California apple industry generally does not place fruit in cold storage so cold treatment is also not considered to be a viable option. Hence, Fuji apples from California are not exported to Mexico. Irradiation, however, may be able to provide an alternative method for California farmers to export Fuji apples to Mexico. It is important, however, that the impact of irradiation on the physiology and subsequent quality of the fruit be fully understood prior to implementation of this treatment.

The objectives of this research were to: 1. Determine if irradiation-induced ethylene suppression is related to membrane damage and loss of ACO activity in Fuji apples. 2. Determine if ethylene suppression affects the normal ripening process as measured by changes in respiration rate, organic acid and sugar concentrations and eating quality (texture and aroma volatiles) of freshly harvested Fuji apples exported to Mexico.

2. MATERIAL AND METHODS

2.1. Fruit procurement, irradiation, and storage

Fuji apples were hand harvested in October 2016 in Linden, CA where the fruit was commercially packed: after washing with food grade soap, brushing and rinsing, the fruits were washed with sodium hypochlorite in a bin dam water system, then sprayed with chlorine dioxide and peracetic acid. After a carnauba wax spray, apples were dried, sorted, and hand-packed into boxes containing 140 fruits distributed in five layers. Apples were stored for three weeks at 1-2 ˚C, before being irradiated with electron beam

at Steri-Tek in Fremont, CA. The electron beams were generated from a 10 MeV, 20 kW Mevex linear accelerator (Stittsville, Canada). Dose mapping was conducted on a dummy box of apples using Gafchromic™ HD-V2 film dosimeters (Ashland Specialty Ingredients, Bridgewater, NJ, USA) placed on either side of 12 apples within the box and a dose uniformity ratio of 1.33 was obtained. The film dosimeters were calibrated against alanine pellet dosimeters (Kodak, Rochester, NY, USA). Verification of dose during the treatments was done by placing a Gafchromic™ dosimeter in a pocket on top of the conveyor rack. The racks were conveyed at different speeds in order to achieve the minimum target doses of 250 and 1000 Gy. The dose that has been approved for apples destined to Mexico is 250 Gy, and in addition we also treated at 1000 Gy, the maximum FDA limit for fresh fruit (CFR, 2018) because a higher dose may be of interest to reduce incidence of fungal decay (Cheon et al. 2016), and also to exaggerate the effects of irradiation because changes in physiology or quality might not be evident at 250 Gy. Apples subjected to a target dose of 250 Gy received an average dose of 377 Gy, while those targeted at 1000 Gy received an average dose of 1148 Gy. Following treatment, all the apple boxes were transported 613 km to Chapman University (Orange, CA) in a refrigerated truck and stored at 0 ˚C and 95% RH for one week in order to simulate transportation from California to Mexico, then another week at ambient temperature (~21 ˚C) to simulate retail conditions in Mexico. Log Tags® (Auckland, New Zealand) were used to track the temperature during treatment, transportation and storage.

2.2. Respiration rate and ethylene production

Respiration rate and ethylene production of apples was measured every two days using the static headspace method described by (Sea et al., 2015). Three sets of eight apples per treatment were allowed to warm up to room temperature (22 °C), then placed in three 3.7 L glass jars covered with size 15 rubber stoppers (Plasticoid Company, Elkton, MD, USA). Three samples of 1 mL gas per jar were withdrawn after 1 h (time previously tested as sufficient to maintain gas levels on the linear range of the accumulation curve) and injected into a gas chromatograph (model # 8610C, SRI Instruments Inc., Torrance, CA, USA) equipped with flame ionizing detector for C_2H_4 and a thermal conductivity detector for CO_2 detection both maintained at 150 °C. Separation was carried out at 80 °C in a 1.83 m x 3.18 mm HayeSep-D (80/100 mesh) column (Restek CO., Bellefonte, PA, USA), using hydrogen as carrier and make up gas at 15 mL min^{-1}. The gases were quantified by measuring peak area in relation to the area of the standards used to create calibration curves.

2.3. Activity of 1-Aminocyclopropane-1-carboxylate oxidase (ACO)

ACO was assayed and calculated following the protocol and equations described by Bulens et al. (2011). The assay was conducted with three replicates per treatment, and ethylene produced was taken from the headspace of two vials per replicate.

2.4. Firmness

Firmness was measured at four points around the equatorial section of six apples for each dose without prior removal of the skin using a Texture Analyzer (Model TA-XT Plus, Stable Micro Systems, Inc., Surrey, UK) with a TA-52, 2 mm cylinder probe, which traveled 10 mm into each sample at a speed of 1 mm s^{-1}. The pre-test and post-test speeds were, respectively, 3 mm s^{-1} and 10 mm s^{-1}. The peak force (N) was recorded and the linear distance (mm) of the force distance curve representing crispiness was calculated between 2 mm and 10 mm of penetration depth.

2.5. Electrolyte Leakage

Electrolyte leakage was measured according to Fan and Sokorai (2005) with some modifications. Six cylinders (9.5 mm diameter/15 mm length) were removed from different points in the cortex of each of ten apples per treatment using a cork borer. The sixty cylinders were randomly divided into three replicates with two subreplicates each, and washed under running deionized water for 5 min and dried on absorbent paper. Samples were incubated for 1 h at room temperature in 50 mL of 0.35 M mannitol solution under shaking at 150 rpm. Electrical conductivity of the solution was measured using a conductivity meter (Labquest 2, Model LQ2-LE Vernier Software and Technology, Beaverton, OR, USA). Samples were then frozen to -80 ˚C for 48 h, rewarmed to 23 ^{o}C, and conductivity was measured again. The relative electrolyte leakage was calculated by dividing the initial conductivity by the reading after thawing and expressed in µS cm^{-1}. The data was averaged for the six replicates per treatment.

2.6. Titratable Acidity and Total Soluble Solids

Ten apples per dose were randomly taken from the storage, peeled and cut into 1 cm dices. The cut apples were separated into three batches before juicing (Elite Gourmet Maxi-matic Juice Extractor TS-738, City of Industry, CA) and filtering through four layers of cheesecloth. Five mL of filtered juice was mixed with 45 mL deionized water and 5% phenolphthalein and titrated with 0.1 N NaOH until color change. Titratable acidity was expressed as % of malic acid. Approximately 0.3 mL of the same juice prepared for TA was used to measure total soluble solids in a Refractometer model Pocket PAL α (Atago, Ltd, Tokyo, Japan). Data from the three replicates was averaged.

2.7. Sensory Evaluation

The tetrad method for difference testing was performed at Chapman University with 39 consumers of apples (age range 21-56 years). The difference test was conducted on the 377 Gy treated apples because this was the closest dose to the 250 Gy dose that has been approved for phytosanitary irradiation of California apples exported to Mexico. Two samples each of freshly cut irradiated (377 Gy) and untreated apples were offered to each participant in plastic containers with lids. The order of sample presentation was randomized to minimize bias. The participants were asked to taste the fruit and pair the identical samples. The responses were recorded and results interpreted using RedJade® Sensory Software.

2.8. Sample Preparation for Chemical Analyses

Six apples, were randomly selected from each of three boxes that received the same treatment (each box was considered one replicate), then peeled, cut into small pieces and frozen instantly using liquid nitrogen and stored at -80 ˚C for subsequent analyses.

2.9. Sugars and Organic Acids

Sugars and organic acids were measured according to Jain et al. (2017). Organic compounds were quantified using calibration curves prepared with three independent sets of dilutions of the corresponding standards.

2.10. Malondialdehyde (MDA)

MDA was extracted and assayed based on the method of Hodges, et al. (1999), and. Malondialdehyde equivalents were calculated using the equations proposed by the same authors.

2.11. Organic volatile compounds

Frozen samples were ground into a fine powder using a cryogenic ball mill (Kleco, Visalia, California, USA). Three g of the powder was added to 9 mL of saturated NaCl in a 20 mL headspace vial (12 mm x 32 mm), ethyl isobutyrate internal standard (final concentration = 61.8 µg L^{-1}) was added and the vial closed with a Teflon-coated septum and vortexed for 30 s. The vials were kept at 4 °C. Volatile analysis was conducted in a similar manner as described by Ummarat et al. (2015) using solid phase microextraction (SPME) with a 75-µm carboxen/polydimethylsiloxane fiber (Supelco, St. Louis, MO,

USA) with the assistance of a Gerstel MPS-2 system (Gerstel, Linthicum, MD, USA) to automate the procedure. Initial equilibration of the sample was at 40 °C for 15 min followed by trapping of volatiles using a SPME fiber for 30 min, using an agitation rate of 4.2 s^{-1}. Trapped volatiles were then desorbed into the splitless inlet (280 °C) of an Agilent 7980 GC (Agilent, Palo Alto, CA, USA) equipped with an Agilent ultra-inert column (30m x 0.25 mm I.D., 0.25 µm film thickness) with a helium flow of 0.02 mL s^{-1}. During the run, oven temperatures were held at 32 ˚C for 3 min, then ramped up to 200 ˚C at 0.1 ˚C s^{-1}. An Agilent 5975C mass spectrometer detector was operated in EI mode to collect mass spectra from *m*/*z* 40 to 200. Compounds were identified using authentic standards if available or by comparison to Wiley/NBS library spectra. Results were semi-quantified by generating calibration curves from standards placed into deodorized apple juice. All standards were purchased from Sigma-Aldrich (St. Louis, MO, USA) with the chemical class and standard utilized for quantification (in parentheses) as follows: ethanol (ethanol), esters (ethyl acetate), alcohols (3-methyl-butanol), aldehydes (E-2-hexenal) and ketones (carvone). Each of the three replicates that were analyzed for each treatment consisted of composite samples from 6 apples.

2.12. Data Analysis

Statistical analysis was conducted using R statistical Software (Team RDC, 2012). A Linear Mixed Effects Model was used to analyze the effects of treatment and storage time on Fuji apples. The effect of treatment within a single time point and the effect of storage time for a specific irradiation dose was analyzed using one-way ANOVA. Two-way ANOVA was used to determine interaction effects of treatment and storage time, and

when significant, Tukey HSD test was used to discriminate differences among treatments or storage time.

3. RESULTS

3.1. Irradiation as inhibitor of ethylene production and ACO activity

Ethylene evolution in untreated apples showed a transient increase from a day after treatment to the fourth day under cold storage (Fig. 1 A). A pronounced increase in ethylene in non-irradiated apples was observed upon removal of the fruits from cold storage one week later likely due to the onset of climacteric, which was delayed in the 377 Gy apples and completely inhibited in apples treated at 1148 Gy. Irradiation decreased the activity of ACC oxidase and it remained significantly lower ($p<0.05$) throughout storage (Fig. 1 B), consistent with the decrease in ethylene production. During storage, ACO activity increased in control apples and apples treated with 377 Gy but did not increase in apples treated with 1148 Gy.

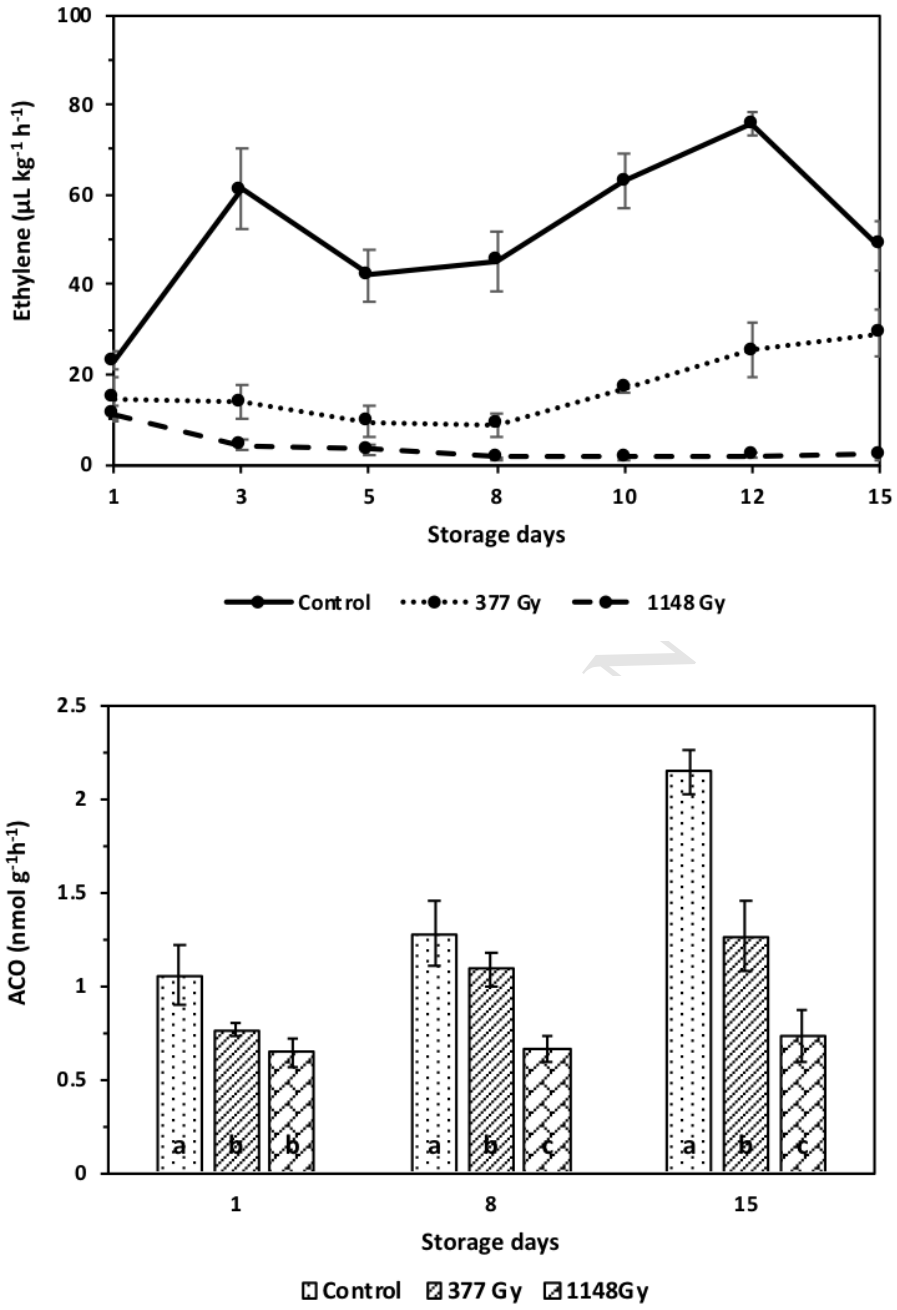

Figure 1 - (A) Ethylene production and (B) ACC Oxidase activity (mean ± SD) in 'Fuji' apples. Ethylene measured every two days after irradiation and ACO on the following day after treatment, after 7 d cold storage (Day 8) and after 7 d ambient storage (Day 15).

Bars labeled with the same letter are not significantly different ($p \geq 0.05$) within each time point.

3.2. Irradiation affecting membrane integrity - electrolyte leakage and MDA production

Treatment with 1148 Gy increased electrolyte leakage by 74%, whereas 377 Gy treated apples showed an increase of 30% one day after irradiation (Fig. 2). There was minimal change during storage in all samples. In irradiated apples, MDA values increased gradually after ambient temperature storage and decreased in control apples (data not shown), but the differences were not significant ($p \geq 0.05$).

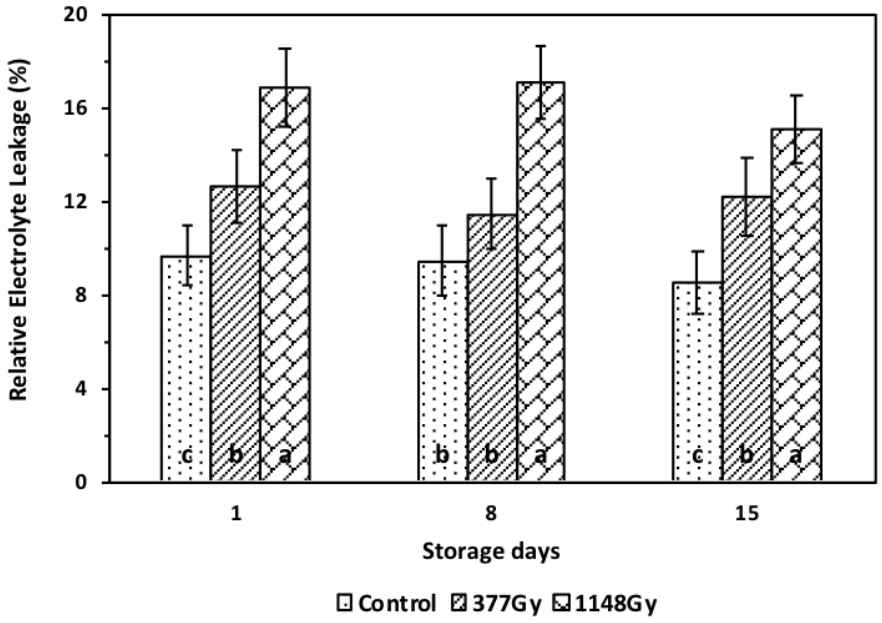

Figure 2 - Relative electrolyte leakage (mean ± SD) in apples the day after treatment (Day 1), after 7 d at cold storage (Day 8) and after 7 d ambient storage (Day 15). Bars labeled with the same letter are not significantly different ($p \geq 0.05$) within each time point.

3.3. **Effect of irradiation on respiration rate, sugars and organic acids**

Irradiation at both doses increased respiration rate immediately after treatment (Fig. 3) which remained higher until the end of the second week at room temperature, when all three treatments had similar respiration rates, at approximately 12.5 mL CO_2 kg^{-1} h^{-1}. Once the fruit was placed in cold storage, a transient peak in respiration was also observed in all treatments, and this burst was relieved by continued cold storage.

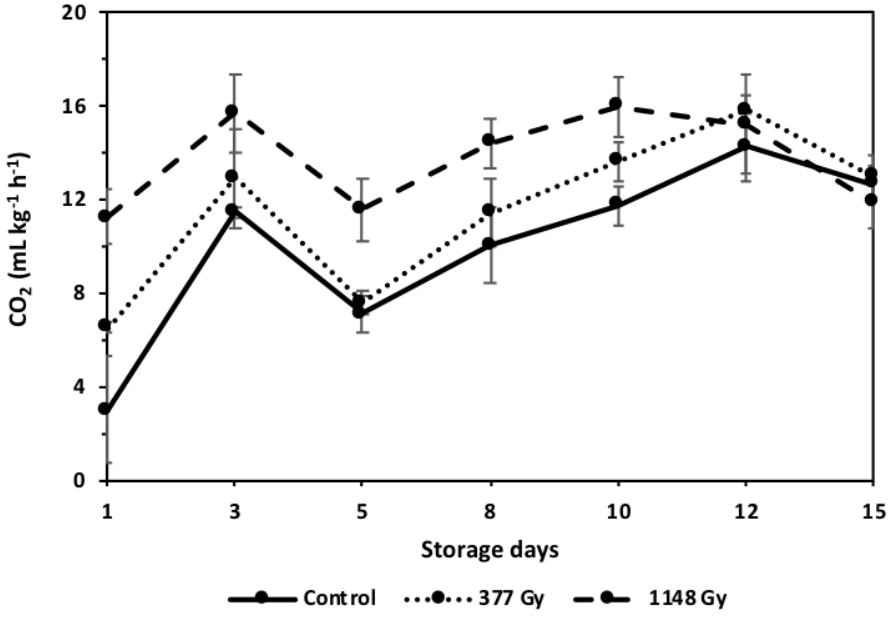

Figure 3 - Respiration rate (mean ± SD) in non-irradiated (control) and irradiated Fuji apples during storage (7 d refrigerated followed by 7 d at ambient).

A small increase in TSS due to irradiation ($p<0.05$) was observed only on day 15 (Table 1). Fructose was the abundant sugar followed by glucose, sucrose and sorbitol (Table 1). Irradiation did not cause immediate changes in titratable acidity (TA), but it was reduced

in 1148 Gy apples during 7 days of cold storage (Table 1). After the apples were placed at room temperature, the TA of the 1148 Gy increased, however no differences among treatments were obvious after 15 days of storage. Malic, shikimic, oxalic and citric acid were quantified in this study (Table 1). A decrease in individual acids was observed in irradiated apples, which remained lower during cold storage. After seven days of storage in ambient temperature, no further differences were observed in malic acid concentrations. This result is consistent with TA values, which is expected since malic acid is by far the most abundant organic acid in apples.

Table 1 - Titratable acidity (TA), total soluble solids (TSS), sugars (fructose, glucose, sucrose, and sorbitol), and organic acids (malic, shikimic, citric and oxalic) in apples the day following treatment (Day 1), after 7 d cold storage (Day 8) followed by 7 d at ambient storage (Day 15).

		Day 1			Day 8			Day 15		
Treatment		**Control**	**377 Gy**	**1148 Gy**	**Control**	**377 Gy**	**1148 Gy**	**Control**	**377 Gy**	**1148 Gy**
TA (%)		2.02 a	1.99 a	1.91 a	1.99 a	1.99 a	1.78 b	1.92 a	1.92 a	1.96 a
Organic Acids (μg g^{-1} FW)	**Malic**	2,370 a	2,650 a	2,510 a	2,700 a	2,640 ab	2,410 b	2,510 a	2,620 a	2,420 a
	Citric	0.55 aB	0.40 bB	0.38 bB	0.82 aA	0.59 bA	0.42 cB	0.43 bB	0.44 bB	0.61 aA
	Oxalic	0.14 aB	0.12 abB	0.11 bB	0.19 aA	0.16 bA	0.12 cB	0.14 bB	0.12 bB	0.18 aA
	Shikimic	7.76 a	6.41 b	6.94 bB	8.45 a	8.00 a	5.74 bB	8.19 a	8.28 a	9.42 aA
TSS (%)		10.13 a	10.25 a	10.55 a	11.00 a	10.75 a	11.13 a	10.13 b	10.57 b	10.85 a
Sugars (mg g^{-1} FW)	**Fructose**	64.69 a	70.84 a	64.89 a	63.91 a	68.63 a	63.29 a	57.91 a	69.68 a	72.46 a
	Glucose	25.68 a	24.52 a	23.95 a	24.57 a	24.68 a	25.53 a	20.84 b	25.47 ab	27.70 a
	Sucrose	9.84 b	16.43 a	9.93 b	9.00 a	12.85 a	10.88 a	6.72 a	11.39 a	9.84 a
	Sorbitol	2.39 a	2.64 a	2.24 a	2.08 a	2.77a	2.28 a	1.44 a	2.34 a	2.73 a

Values labeled with same lower case are not significantly different ($p \geq 0.05$) within each time point. Same uppercase letters indicate that differences are not significant among evaluation times.

3.4. Influence of irradiation on firmness, aroma and consumer perception

Irradiation at 377 Gy and 1148 Gy reduced firmness immediately after treatment by 11.78% and 35.61%, respectively (Fig. 4). The removal of apples from cold storage after 7 days did not further influence firmness.

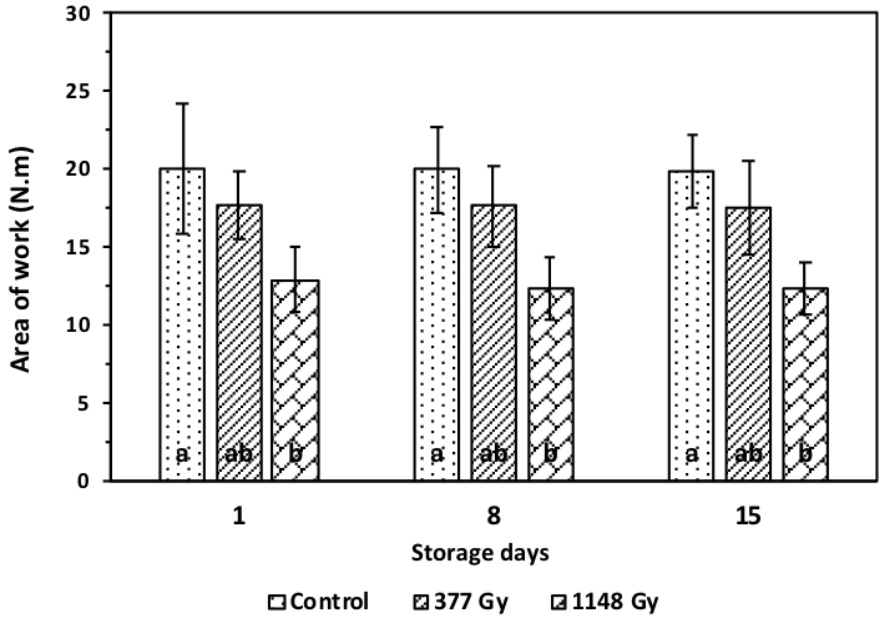

Figure 4 – Firmness (mean ± SD), expressed as area under the force × distance curve, in apples the day after treatment (Day 1), after 7 d cold storage (Day 8) and after 7 d ambient storage (Day 15). Bars labeled by the same letter are not significantly different ($p \geq 0.05$) within each time point.

There were 42 volatiles that were identified but only the 32 that were found to statistically differ ($p<0.05$) due to irradiation treatment are shown in Table 2. There was

far less overall effect of irradiation at 377 Gy on the measured volatiles immediately following treatment relative to 1148 Gy. Ethanol production increased in apples subjected to 1148 Gy after 8d and in apples exposed to both doses after 15 d. The effect of 1148 Gy irradiation on esters was mixed with some esters increasing and others decreasing in concentration. Following 14 d of storage, irradiation was inhibitory for most of the esters.

Table 2 - Aroma volatile concentrations (µg L^{-1}) in apples the day after treatment (Day 1) and after 7 d cold storage (Day 8) followed by an additional 7 d ambient storage (Day 15).

	Day 1			Day 8			Day 15		
	Control	377 Gy	1148 Gy	Control	377 Gy	1148 Gy	Control	377 Gy	1148 Gy
Alcohols									
ethanol	9,079.8b	10,635.2b	20,379.4a	9,051.3b	10,361.5b	27,129.0a	7,543.6c	12,399.7a	9,752.6b
butanol	1,133.2a	1,111.9a	1,087.1a	874.9b	1,196.6a	758.4b	761.0ab	1,051.4a	656.4b
hexanol	2,991.8a	3,003.7a	2,292.4a	2,069.5a	2,566.8a	1,353.2b	1,423.4b	2,189.2a	1,038.0b
Aldehydes									
acetaldehyde	5.6a	7.0a	7.7a	6.6a	6.2a	5.5a	5.2b	8.1a	6.5ab
butanal	7.7a	8.0a	4.8a	6.7b	11.5a	3.8b	5.6a	7.3a	2.5b
pentanal	3.5a	4.0a	4.5a	3.3b	3.9b	5.9a	2.5b	4.3ab	5.1a
2,4-hexadienal	25.2a	20.5a	16.7a	24.0a	18.3a	18.4a	15.9ab	22.2a	13.8b
nonanal	17.8b	16.0b	27.6a	18.0b	18.8b	24.8a	15.0a	25.8a	20.6a
Esters									
ethyl acetate	14.1b	15.9b	157.9a	16.4b	16.9b	258.9a	28.0a	50.5a	9.8a
propyl acetate	52.3b	56.0b	138.1a	70.3b	74.3b	177.4a	57.1b	86.2a	31.7c
methyl butanoate	21.9a	13.7b	19.9a	51.7a	21.8b	35.0ab	105.4a	45.8b	13.9c
isobutyl acetate	21.6a	26.5a	32.9a	28.3b	32.8ab	38.5a	23.6a	29.6a	31.8a
butyl acetate	3,391.0a	2,653.5a	2,669.7a	4,446.9a	2,992.0ab	1,556.3b	5,680.5a	4,182.7a	655.2b
isopropyl butanoate	16.0a	10.7ab	3.9b	13.9a	9.5b	3.6c	14.2a	10.8a	3.3b
ethyl 2-methylbutanoate	13.7b	16.1b	299.7a	16.5b	15.3b	243.9a	18.7a	34.7a	10.0a
2-methylbutyl acetate	2,767.2a	2,551.2a	3,506.7a	3,948.6a	3,343.4a	2,303.6b	3,762.2a	3,704.3a	1,482.5b
propyl butanoate	331.4a	156.1b	181.3b	385.0a	215.4b	172.9b	253.5a	207.9a	33.6b
butyl propanoate	94.3a	139.5a	122.4a	150.3a	211.8a	68.0b	153.5a	193.4a	22.5b
isoamyl acetate	349.3a	283.7a	299.2a	353.5a	274.5a	187.4b	495.5a	439.3a	141.6b
methyl hexanoate	9.8a	9.1a	8.6a	12.3a	13.7a	10.8a	30.8a	24.6ab	7.3b
isobutyl butanoate	13.2a	8.0b	5.1b	14.1a	9.8ab	4.2b	11.3a	9.6ab	3.8b
butyl butanoate	1,049.1a	728.1ab	380.7b	1,009.2a	755.7a	259.2b	994.6a	777.4a	149.2b
ethyl hexanoate	64.4b	72.5b	173.7a	47.5b	69.7b	132.3a	120.7a	141.3a	15.0b
hexyl ethanoate	4,111.2a	2,896.2a	2,647.8a	3,136.0a	2,440.9a	1,104.1b	4,693.2a	4,011.9a	722.6b
isopropyl hexanoate	13.2a	9.2b	11.0ab	10.2a	9.6a	9.7a	10.8a	9.7a	7.2a
butyl 2-methylbutanoate	201.7b	160.7b	318.8a	214.4a	156.9b	147.2b	203.2a	181.5a	63.2b
hexyl butanoate	771.8a	587.9ab	282.3b	559.1a	549.7a	166.2b	506.5a	541.9a	124.7b
hexyl 2-methylbutanoate	98.5a	88.2a	162.5a	85.2a	84.6a	73.9a	77.4ab	96.4a	48.8b
hexyl hexanoate	61.8a	65.1a	18.7b	37.4a	48.2a	12.3b	33.5ab	50.2a	11.0b
Ketones									
4-methyl-2-heptanone	0.6b	1.0b	2.0a	0.8a	1.1a	1.6a	0.7a	1.3a	0.8a
1-octen-3-one	3.3a	3.0a	3.1a	3.6b	2.6b	7.3a	2.6a	4.5a	4.8a
6-methyl-5-hepten-2-one	9.4a	8.4a	7.9a	11.3a	8.9b	10.6ab	8.9a	11.6a	7.8a

Values followed by different letters within a storage regime are significantly different ($p<0.05$).

Dark grey cells highlight increase compared to the control, light grey show decrease from the control.

3.5. Sensory Analysis

Fifty seven percent of the consumers were able to pair the identical samples, which was not significant at a confidence level of 0.05%. This means that consumers could not tell the difference between the control and 377 Gy samples.

DISCUSSION

An initial and transient increase in ethylene production observed in all apples could be related to the stress of handling and transportation with subsequent attenuation by cold storage. The inhibition of ethylene production by irradiation was accompanied by concomitant decreases in ACO activity (Fig. 2B), suggesting an inactivation effect of irradiation on ACC oxidase enzyme. Irradiation-induced inhibition of ethylene production has been also observed in Gala apples treated at 440 and 1320 Gy (Fan et al., 2001). In breaker tomatoes, Larrigaudière et al. (1990) reported inhibition of ACO at doses of >1000 Gy and suggested that an impairment in membrane functions caused by irradiation would directly affect ACO activity. The subcellular localization of ACO it still unclear. Although studies with apples (Ramassamy et al. 1998) and tomatoes (Rombaldi et al. 1994) have determined the enzyme to be membrane-bound, other immunolocalization studies reveal a cytoplasmic destination for the ACO protein in apples (Chung et al. 2002). Still, ethylene perception is regarded as a membrane-dependent process since ethylene receptors are associated with membranous structures, therefore, an impairment in ethylene production may be regarded as an indirect response to membrane damage by irradiation.

The immediate increase observed in electrolyte leakage (EL) upon irradiation suggests a physical impact of irradiation on membrane structure. Fan and Sokorai (2005) also observed a linear increase in EL in various vegetables irradiated at doses up to 3000 Gy. As electrolyte leakage was higher in irradiated apples, higher MDA concentration was also expected, but this was not the case. MDA results may indicate that Fuji apples did not show evident symptoms oxidative stress at the doses and storage conditions in this study, or the method for measuring MDA used in this work was unable to reflect biochemical changes occurring in membranes as a consequence of irradiation. Voisine et al. (1991) also reported that irradiation treatment of cauliflower caused pronounced increase in electrolyte leakage but small changes in membrane lipid composition. Hayashi et al., (1992) observed increased electrolyte leakage within one hour of irradiating potatoes at 1 kGy with changes in phospholipid content and glycolipid composition occurring in subsequent weeks, which suggests the possibility that MDA changes might have been observed if the storage period of the irradiated apples of the present work was extended beyond two weeks.

Increased respiration rate was observed in all samples, independent of treatment, which could also be related to the stresses of handling, transportation and temperature fluctuations in this experiment. The strongly inhibited ethylene production and highest respiration rate in apples treated at 1148 Gy are indicators of a contribution of factors other than ethylene to the initial stress response upon irradiation (Fig. 1). Similar to our results, Massey Jr et al. (1964) observed that irradiation at 500 and 1148 Gy increased respiration rate of ‘Rome Beauty’ and ‘Macintosh’ apples during two weeks of storage at 21˚C. Catabolism of acetate and stimulation of enzymes of the Krebs cycle by irradiation

has been suggested as the cause for higher CO_2 evolution (Massey Jr and Bourke, 1967). Romani et al. (1968) showed that respiration rate as a response to irradiation depends on the maturity stage, proposing that tissues irradiated at the pre-climacteric stage are able to induce energy requiring repair mechanisms that reflects in higher respiratory activity.

In this study, irradiation enhanced the respiration rate and inhibited ethylene production, however TSS and individual sugars were initially not impacted, similar to the observations of Fan and Mattheis (2001) for Gala apples treated up to 1320 Gy and Drake et al. (1999) for Fuji, Granny Smith and Gala apples treated at 900 Gy, and Jung et al., (2016) for Fuji apples irradiated up to 1000 Gy. According to Dandekar et al. (2004), apple fruits from transformed plant silenced for both ACC synthase and ACC oxidase genes did not show significant change in sugars and acids, suggesting that changes in these quality parameters are not under direct control of ethylene. In contrast to sugars, TA and organic acid concentrations were affected by irradiation dose. Drake et al. (1999) found that the effect of irradiation at 0-900 Gy on TA was cultivar dependent and reduction in TA was observed in Gala apples, while Fuji and Granny Smith varieties were not affected by irradiation. The decrease observed in TA values was also reflected in individual acids and can be related to the higher initial respiration rate of the irradiated apples and consumption of acids as substrate in TCA cycle (Al-Bachir 1999). During cold temperature storage, the increase in oxalic and citric acids in the control and 377 Gy apples can be attributed to continued glycolysis and the hydrolysis of sugar substrates to form acids, while decrease during ambient storage is likely due to the onset of climacteric respiration in these apples.

On the other hand, irradiation at 1148 Gy caused an initial decrease in oxalic and citric acids, with subsequent increase during climacteric rise. The high dose may temporarily inhibit enzymes of the glycolytic pathway, resulting in decreased amount of organic acids. Inhibition of the glycolytic pathway may also be responsible for the reduction in shikimic acid, an important intermediate derived from glycolysis and pentose phosphate pathway. After storage for 15 days, a possible recovery from the impact of irradiation with lower utilization of shikimic acid in the phenylpropanoid pathway could be responsible for the increase in shikimic acid content in irradiated apples (Khanam, 2007; Reyes and Cisneros-Zevallos, 2007).

Similar to our results, a dose-dependent softening after irradiation was also observed by Drake et al. (1999) in Fuji apples treated at 300, 600 and 900 Gy (~4%, ~5% and 12% respectively). Massey Jr et al. (1964) and Al-Bachir (1999) correlated loss of firmness in irradiated apples to the breakdown of insoluble pectate fractions into soluble forms, while Kovacs et al. (1988) observed breakdown of middle lamellae and wrinkling of cell membranes which remained structurally preserved. In Golden Delicious apples, low-dose irradiation (300-600 Gy) maintained firmness during nine-month storage, while high doses (900-1000 Gy) caused firmness loss, which was associated with increased water and oxalate soluble pectins (Mostafavi et al., 2012).

Volatile compounds were likely affected by the increased respiration rates and decreased ethylene production, especially at the highest irradiation dose. Higher respiration with reduced diffusion rates through the fruit skin are associated with the depletion of internal O_2 concentrations in some fruits such as tomatoes (Speirs et al., 1998) and mandarins (Shi et al., 2007) leading to enhanced gene expression of the alcohol dehydrogenase

(ADH) enzyme, therefore, increasing the levels of ethanol in the tissues. Values measured in this work were consistent with those found by Song et al. (2012) in Fuji apples, especially for butyl esters and aldehydes. Fan et al. (2001) observed a decrease in total esters in 'Gala' apples subjected to doses of 880 and 1320 Gy and stored for 20 days at 20 ^{o}C, similar to the results found in this study. Suppression of ethylene synthesis and action has been shown to reduce the synthesis of aroma volatiles in climacteric fruits (El-Sharkawy et al., 2005; Fan et al., 1998; Fan et al., 2001). Thus, with the exception of some esters which increased during cold storage, the inhibition of volatiles observed after storage at higher temperature can be related to the low levels of ethylene in the 1148 Gy apples.

Similar to firmness and volatiles, the impact on sensory attributes appears to be strongly dependent on dose. Fuji apples treated up to 600 Gy had few sensory changes as compared to control apples, but irradiation at 1000 Gy made off-flavors and softening of the flesh perceptible to the sensory panel and overall acceptance was reduced (Jung et al. 2016). In our study, consumers were unable to tell the difference between control and 377 Gy showing that the changes in firmness and volatiles were not severe enough to impact sensory attributes.

4. CONCLUSIONS

Irradiation resulted in decreased ethylene production and activity of ACC oxidase at 377 Gy and strong inhibition with loss of the climacteric respiratory peak at 1148 Gy. The decrease in ACC oxidase might be associated with physical rather than biochemical damage to membranes as evident by the higher electrolyte leakage and unchanged MDA

concentration in 1148 Gy irradiated apples. Irradiation at the highest dose inhibited synthesis of volatile compounds, especially esters after 7 d of cold storage followed by 7 d of ambient storage while irradiation at 377 Gy following either storage regime had far less impact on any of the measured volatiles. Texture was the only major quality attribute impacted by irradiation, however consumers were not able to tell the differences between control and 377 Gy apples. The lack of perceived changes in texture, and small differences in sugar and acid composition caused by irradiation show that the low levels of ethylene remaining after irradiation are sufficient to induce normal maturation processes in apple fruit. Future research should be conducted on understanding how irradiation as an abiotic stress could affect gene expression of ethylene biosynthetic enzymes and the relation between membrane damage and the decrease in the activity of ACO and other enzymes in the ethylene biosynthetic pathway such as 1-aminocyclopropane-1-carboxylate oxidase synthase (ACS) in apples.

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Declaration of Interest

There are no conflicts of interest.

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Physiological response of 'Fuji' apples to irradiation and the effect on quality

Nasim Kheshti[a], Anderson Adriano Martins Melo[a,*], Alan Baquero Cedeno[a], David Obenland[b], Anuradha Prakash[a]

[a]Chapman University, Food Science Department, One University Drive, Orange CA 92866, USA.

[b]USDA, Agricultural Research Service, San Joaquin Valley Agricultural Sciences Center, 9611 South Riverbend Avenue, Parlier CA 93648-9757, USA. *Corresponding author.

Highlights

- Irradiation at 377 Gy decreased ethylene production and activity of ACC oxidase.
- Decreased ACC oxidase activity might be associated to physical damage in membranes.
- Irradiation at 1148 Gy inhibited synthesis of volatiles after cold-ambient storage.
- Consumers were not able to tell the differences between control and 377 Gy apples.