Variation among Strawberry Cultivars in Bruising Susceptibility Related to Wound Ethylene Production and Sensitivity

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Additional index words. calyx yellowing, decay, *Fragaria × ananassa*, mechanical injury, respiration, water soaking

Abstract. Bruising of strawberry (*Fragaria × ananassa* Duch.) fruit is a common mechanical injury that reduces product value. Wound-induced ethylene may accelerate deterioration or decay, affecting strawberry quality and shelf life. However, bruising susceptibility varies among strawberry cultivars. In this study, cultivars Monterey, Sweet Sensation, Radiance, and two proprietary cultivars (Cultivar A and Cultivar B) from a private breeding program were investigated to evaluate their bruising susceptibility and wound response. Bruising consisted of dropping a 28-g steel ball from 27 cm onto individual fruit; unbruised fruit were the primary control, while fruit exposed to 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene were used as a check for ethylene response. All fruit were stored at 20 °C, 90% relative humidity (RH), with respiration and ethylene production measured at 2-hour intervals for 24 hours. Appearance observations were recorded daily until decay onset. Peak respiration rates of 30–40 $\text{mL CO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ mostly occurred within 4 hours ('Cultivar B') to 6 hours ('Cultivar A' and 'Sweet Sensation') after bruising, except 'Monterey', which peaked at 60 $\text{mL CO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ in 2 hours, and 'Radiance', which reached 70 $\text{mL CO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ in 6 hours. Maximum ethylene production rates after bruising were 0.05 to 0.06 $\mu\text{L}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for 'Monterey', 'Cultivar A', and 'Cultivar B', 0.10 $\mu\text{L}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for 'Sweet Sensation', and 0.20 to 0.37 $\mu\text{L}\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ for 'Radiance'. 'Cultivar B', with the lowest ethylene production, exhibited the lowest overall bruising severity, whereas 'Radiance', with the highest ethylene production, exhibited the most severe bruising-induced water soaking, and the other cultivars were intermediate, although 'Monterey' bruises were more discolored than those of the other cultivars. 'Monterey', 'Radiance', and 'Sweet Sensation' showed more yellowing and browning of the calyx in response to both bruising and ethylene exposure than 'Cultivar A' and 'Cultivar B'. Except for 'Cultivar B', bruising and ethylene exposure increased decay severity.

Strawberry (*Fragaria × ananassa* Duch.), the third most consumed fresh fruit in the U.S. market in 2017 (USDA, 2019), is attractive and highly valued, but it is delicate. Large cells with thin cell walls result in the fragile structure of strawberry fruit (Szczesniak and Smith, 1969), which become more susceptible to mechanical injury as the ripening process proceeds. Strawberries are harvested when mostly or fully ripe according to the commercial standard for U.S. No. 1 grade, which states that strawberry fruit must be at least 3/4 red (USDA, 2006). Bruising occurs mainly during harvesting, packing, and transportation for hor-

tical crops (Prussia and Shewfelt, 1993). When plant tissues are wounded, the physical and metabolic reactions change in the damaged tissues and trigger ethylene production, resulting in major postharvest losses, decay, and accelerated senescence, thus affecting strawberry quality and shelf life (Ferreira et al., 2009; Wills and Kim, 1995). The severity of wounding in strawberry depends on various factors, including the type of force applied on the fruit, cooling method, and rate of lowering pulp temperatures, along with the storage temperature (Ferreira et al., 2009). Internal fruit properties, such as texture, fruit maturity, water content, firmness, size, and shape (Hung and Prussia, 1989; Van Linden et al., 2006), and the nature of cultivars (Jiménez-Jiménez et al., 2013; Kunze et al., 1975) also contribute to the bruising response. Bruising severity and the tissues being affected can be determined by dissecting the fruit and measuring the bruise diameter, depth, and volume, which have strong positive correlations with impact energy (Schoorl and Holt, 1980).

Mechanical injury, such as cutting, abrasion, or bruising, has been shown to cause

climacteric fruits such as banana and tomato to produce an increasing amount of ethylene (Moretti et al., 1998; Palmer and McGlasson, 1969). However, strawberry fruit is often regarded as a nonclimacteric and ethylene-insensitive crop. In previous research, some researchers have suggested that ethylene could not only stimulate the respiration rate of nonclimacteric fruit, but also accelerate fruit color development, softening, and ion leakage, with a deleterious logarithmic linear response to 10 to $<0.005 \mu\text{L}\cdot\text{L}^{-1}$ ethylene in terms of shelf life (Wills and Kim, 1995; Wills and Wong, 1996; Wills et al., 1999). In contrast, other researchers have presented evidence showing little or no effect of ethylene on strawberries (El-Kazzaz et al., 1983; Tian et al., 2000). The role of ethylene in nonclimacteric fruit wounding response is uncertain, and the differential response toward ethylene in previous studies was reported to be affected by maturity, storage time, and cultivar characteristics (El-Kazzaz et al., 1983; Picón et al., 1993; Tian et al., 2000).

In tests to determine the potential benefits of removing ethylene from the strawberry postharvest environment that were conducted before the present research (Brecht et al., 2016), we observed significant cultivar variation in response to ethylene scrubbing in terms of bruising severity and calyx yellowing and browning. We hypothesized that those differences in response to ethylene scrubbing might be related to differences in wound ethylene production or ethylene sensitivity among the cultivars that had been tested. Therefore, in this study, several major commercial strawberry cultivars, including Monterey, Sweet Sensation (Florida 127), Florida Radiance, and two proprietary cultivars (Cultivar A and Cultivar B) from a private breeding program, were investigated to determine their bruising susceptibility and wound response in terms of timing and the rate of wound ethylene production to inform further improvements in postharvest procedures.

Materials and Methods

Plant material. Strawberry fruit of the University of California licensed cultivar Monterey (received 24 Oct. 2017), two cultivars licensed by the University of Florida, namely Sweet Sensation (Florida 127) (Sweet Sensation) (received 11 Dec. 2017) and Florida Radiance (Radiance) (received 21 Mar. 2018), and two proprietary cultivars, Cultivar A (4 Oct. 2017) and Cultivar B (11 Dec. 2017), were received from distribution centers of retailers at the beginning of the harvest season for each variety and immediately transported to the University of Florida Postharvest Horticulture Laboratory in Gainesville by air-conditioned van at $\approx 18^\circ\text{C}$ within 2 h. Five separate experiments were conducted. Additional experiments conducted with 'Radiance' (once) and 'Sweet Sensation' (twice) showed similar results and are not presented here. On arrival at the laboratory, fruit were stored at

Received for publication 15 Nov. 2019. Accepted for publication 3 Jan. 2020.

Published online 25 February 2020.

We thank It's Fresh Ltd. for their support by providing research funding for this work.

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Fig. 1. Time course within 24 h for the respiration rate of (A) 'Cultivar A', (B) 'Cultivar B', (C) 'Monterey', (D) 'Radiance', and (E) 'Sweet Sensation' fruit with control (CK, solid line) and bruised (Bruised, dash line) fruit during storage at 20 °C and 95% relative humidity. Each data point represents the mean of three observations. Vertical bars represent SE.

1 °C overnight to reduce the disturbance of the physiological response during transportation. Fruit were rewarmed to ambient temperature (24 °C) the following day and fully red fruit, selected for uniform color, size, and freedom from defects, were grouped into three replicate groups of similar weight per cultivar (900 g for 'Cultivar A', 800 g for 'Monterey', and 650 to 670 g for 'Sweet Sensation', 'Radiance', and 'Cultivar B').

Treatments. To examine whether the wound response in strawberry fruit involves ethylene, bruised fruit (BR), fruit treated with 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene (ETH), and untreated fruit as control (CK) were used in the experiments. Bruising treatment followed the procedure of Ferreira et al. (2008) with modifications to deliver the same impact energy to the fruit. A 28-g steel ball was released from a height of 26.67 cm within a plastic tube directed to the proper impact point on individual fruit at 24 °C on the fullest part of the side of the fruit; the applied impact energy was ≈ 0.74 J.

Then, the BR fruit and the unbruised treatments (CK and ETH) were collected in rigid plastic clamshell containers as experimental units and stored at 20 °C. For ethylene application, three experimental units were placed in a 20-L closed plastic bucket at 20 °C and ventilated with air with $\approx 95\%$ to 100% RH containing 1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene for 24 h. The other three unbruised units were regarded as CK. The CK and BR treatments were placed in separate ventilated chambers at 20 °C with humidity $\approx 95\%$ to 100% RH. The ETH treatment was transferred to identical ventilated chambers after the 24-h ethylene application for further observation.

Assessment of respiration and ethylene production. Containers of BR and CK fruit were sealed for 1 h at each 2-h interval during the first 24 h of each experiment. Ethylene and carbon dioxide concentrations were determined by injecting a 3-mL sample of headspace into a Varian CP-3800 gas chromatograph (Varian Inc., Walnut Creek, CA)

equipped with a pulsed discharge helium ionization detector (PDHID) and a thermal conductivity detector (TCD). Using an automated sample-loop and valve system, a 1-mL portion of the injected sample for ethylene determination passed through Hayesep Q Ultimet (1 m $\times$ 3.18 mm) [particle size, 149–177 μm (80/100 mesh)] and Hayesep Q Ultimet (1 m $\times$ 3.18 mm) [particle size, 149–177 μm (80/100 mesh)] columns (Varian) coupled in series to the PDHID. Another portion (1 mL) of the injected sample for CO_2 determination passed through Hayesep Q Ultimet (1 m $\times$ 3.18 mm) [particle size, 149–177 μm (80/100 mesh)] and Molsieve 13 (1.5 m $\times$ 3.18 mm) [particle size, 149–177 μm (80/100 mesh)] columns (Varian) coupled in series to the TCD. The carrier gas (helium) flow rate was 0.25 $\text{mL}\cdot\text{s}^{-1}$. The injector and oven were operated at 220 °C and 50 °C, respectively. The PDHID was operated at 120 °C and the TCD was operated at 130 °C.

Assessment of wound response. At 24 h after treatment, the bruise diameters of each fruit were measured from edge to edge on two perpendicular axes with a caliper and averaged. Defects of BR, CK, and ETH strawberry fruit, including the bruised area on BR fruit, water soaking or darker color of bruised areas, calyx degreening, and decay were photographed and evaluated for each fruit at 24 h after treatment and daily until the onset of decay using the incidence rates of the defects. Evaluations of bruising symptoms for CK and ETH treatments were performed for incidentally bruised areas that were not evident during initial sorting because those fruit had not been intentionally bruised like the BR fruit.

Statistical analysis. Carbon dioxide and ethylene production rate data over time were analyzed by a one-way repeated measure analysis of variance (ANOVA) of each cultivar, and bruise diameters among cultivars were analyzed by one-way ANOVA with the JMP Pro 14.1.0 (SAS Institute, 2019) software and Microsoft Excel (version 1910; Microsoft Office 365; Microsoft, Redmond, WA). Fisher's least significant differences ($P \leq 0.05$) were determined to compare differences between treatment means following a significant ANOVA effect. Mean data are presented ($\pm$ SEM).

Results and Discussion

Respiration and ethylene production during the first 24 h after treatment among different cultivars. Bruising treatment stimulated respiration of all cultivars. Respiration rates for each cultivar differed (Fig. 1), with 'Radiance' having the highest rate, followed by 'Monterey', 'Cultivar A', and 'Cultivar B'; 'Sweet Sensation' had the lowest rate. Peak respiration rates of 34.14 and 45.38 $\text{mL}\cdot\text{CO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ occurred at 6 h after bruising for 'Sweet Sensation' and 'Cultivar A', respectively, and 42.47 $\text{mL}\cdot\text{CO}_2\cdot\text{kg}^{-1}\cdot\text{h}^{-1}$ occurred at 4 h after bruising for 'Cultivar B'. Peak respiration rates after bruising for 'Monterey'

Fig. 2. Time course within 24 h for the ethylene production rate of (A) 'Cultivar A', (B) 'Cultivar B', (C) 'Monterey', (D) 'Radiance', and (E) 'Sweet Sensation' fruit with control (CK, solid line) and bruised (Bruised, dash line) fruit during storage at 20 °C and 95% relative humidity. Each data point represents the mean of three observations. Vertical bars represent se.

Table 1. Bruise diameters of 'Cultivar A', 'Cultivar B', 'Monterey', 'Radiance', and 'Sweet Sensation' stored at 20 °C and 95% relative humidity measured 24 h after bruising.

Cultivar	Bruise diam (mm)
Cultivar A	12.34 ± 0.55 a ²
Cultivar B	8.98 ± 0.22 c
Monterey	10.55 ± 0.39 b
Radiance	9.10 ± 0.20 c
Sweet Sensation	9.03 ± 0.26 c
LS _D 0.05	1.34

²Means followed by the same letter in the column are not significantly different according to the least significant difference (LSD) test ($P > 0.05$). $n = 15$ fruits.

(59.58 mL CO₂·kg⁻¹·h⁻¹ in 2 h) and 'Radiance' (78.63 mL CO₂·kg⁻¹·h⁻¹ in 6 h) were higher than those for the other cultivars. Respiration rates of 'Radiance' and 'Monterey' were also significantly higher than those for the other cultivars over the entire 24 h after treatment.

Ethylene production was slightly higher in BR fruit in most cultivars except for Cultivar B, which maintained relatively low ethylene production in both BR and CK (Fig. 2). Among the cultivars, ethylene production was highest for 'Radiance', followed by 'Sweet Sensation' and 'Cultivar A', 'Cultivar B', and 'Monterey'. Maximum ethylene production after bruising occurred at ≈4 h, up to 0.060 μL·kg⁻¹·h⁻¹ in 'Monterey', 0.056 μL·kg⁻¹·h⁻¹ in 'Cultivar A', 0.066 μL·kg⁻¹·h⁻¹ in 'Cultivar B', 0.10 μL·kg⁻¹·h⁻¹ in 'Sweet Sensation', and 0.37 μL·kg⁻¹·h⁻¹ in 'Radiance'. There were different numbers of fruit of each cultivar in each replicate due to variations in fruit size, which meant there were different numbers of applied bruises per replicate. Therefore, we also calculated the respiration and ethylene production rates on a per fruit basis, but this did not reveal any differences in the relative rates for the bruised vs. unbruised treatments or between the cultivars (data not shown).

The ethylene production after 12 h for 'Cultivar A', 'Monterey', 'Sweet Sensation', and 'Radiance' increased up to 2- to 10-fold, presumably due to the development of decay caused by gray mold (*Botrytis cinerea*). Infection of *B. cinerea* has been reported to accelerate the ethylene production by the affected host plant tissues and by the fungus itself, with ethylene promoting decay of nearby tissues or fruit (Chague et al., 2002; Qadir et al., 1997).

Tian et al. (2000) indicated that enhanced respiratory rate in response to exogenous ethylene exposure depended on the ethylene concentration and the treatment duration, with fruit treated with 1 μL·L⁻¹ ethylene for 2 d observed to produce more CO₂. Even though ethylene production rates for 'Radiance' and 'Monterey' in the present work were comparatively higher than those for the other cultivars, it did not appear to affect the respiration rate. However, ethylene and CO₂ production rates of 'Sweet Sensation' increased synchronously after 16 h (Figs. 1C and 2C), which might have been due to greater sensitivity to ethylene in that cultivar.

Comparison of appearances among different treatments within each cultivar. Bruise diameters measured at 24 h after bruising were significantly larger for 'Cultivar A' and 'Monterey' compared with 'Cultivar B', 'Radiance', and 'Sweet Sensation', which were not significantly different from each other (Table 1).

Defects among cultivars and treatments were categorized into four major symptoms, including decay, calyx yellowing or browning, fruit with water soaking, and fruit with darker damaged areas (Table 2). Decay was mostly represented by *Botrytis* fruit rot (gray mold), which manifested the symptoms of light brown spots or gray fuzzy coating on the fruit surface. Decay developed more rapidly in 'Cultivar A', 'Monterey', and 'Radiance' than in 'Cultivar B' and 'Sweet Sensation'. Fruit of 'Cultivar B' had the least amount of fruit infected by the fungus, whereas 'Monterey' and 'Radiance' were more susceptible.

The growth of *B. cinerea* was expected to be accelerated by 20 μL·L⁻¹ ethylene (El-Kazzaz et al., 1983). 'Radiance' produced the most ethylene among the cultivars, and the BR fruit maintained ethylene production at higher rates than the CK fruit. After the initial wound ethylene production following bruising, an additional increase in ethylene production started after 12 h, which was associated with accelerated fungal growth. Initial ethylene production of 'Monterey' was relatively low, at ≈0.03 μL·kg⁻¹·h⁻¹, but the production increased starting from the sixth hour, with BK fruit producing more ethylene than CK fruit, which may have been related to enhanced growth of the fungus. However, neither bruising treatment nor ethylene exposure consistently promoted decay in the strawberry cultivars tested (Table 2). 'Cultivar B', which did not exhibit increased ethylene production in response to bruising, also did not exhibit increased decay in either the BR or the ETH treatments, whereas 'Sweet Sensation' showed increased decay

Table 2. Severity ratings of strawberry defects after bruising or ethylene treatment evaluated at the onset of decay.

Cultivar	Days before decay onset	Major defects ^a			
		Decay	Calyx yellowing/browning	Fruit water soaking	Fruit with darker damage area
Cultivar A					
Control	2	1	2	2	1
Bruised (0.74 J)		3	3	3	2
Ethylene (1 ppm)		3	3	2	2
Cultivar B					
Control	3	2	2	1	1
Bruised (0.74 J)		2	2	2	1
Ethylene (1 ppm)		2	3	2	1
Monterey					
Control	2	3	2	1	2
Bruised (0.74 J)		4	4	2	3
Ethylene (1 ppm)		4	4	2	3
Radiance					
Control	2	3	2	2	2
Bruised (0.74 J)		4	4	4	1
Ethylene (1 ppm)		4	4	2	1
Sweet Sensation					
Control	3	2	4	0	1
Bruised (0.74 J)		4	5	1	1
Ethylene (1 ppm)		2	5	0	2
Least significant difference at $P = 0.05$		0.71	0.64	1.29	0.50
Cultivar		****	****	****	****
Treatment		****	****	*	**
Cultivar × treatment		**	NS	NS	****

^aThe proportion of total fruit presenting symptoms: 1: 0% to 20%; 2: 21% to 40%; 3: 41% to 60%; 4: 61% to 80%; 5: 81% to 100%. n = 3.

NS, *, **, ***, ****Nonsignificant or significant at $P = 0.05, 0.01, 0.001$, or 0.0001 , respectively, according to the F-test.

in response to bruising, but not to ethylene exposure. These results indicate that for some strawberry cultivars, the amount of ethylene required to accelerate the growth of *B. cinerea* might be lower than the $20 \mu\text{L}\cdot\text{L}^{-1}$ ethylene reported previously by El-Kazzaz et al. (1983), but ethylene may have a small or no role in the development of Botrytis rot in other cultivars. However, the reduced levels of both wound ethylene production and decay observed in 'Cultivar B' suggest that the selection of strawberry germplasm with reduced wound ethylene production may represent an avenue for developing strawberry cultivars with reduced postharvest decay.

'Monterey' fruit had the most yellowing and browning of the calyx in the BR and ETH treatments, followed by 'Radiance' and 'Sweet Sensation' (Table 2). Cultivar A and Cultivar B exhibited less calyx yellowing and browning than the other cultivars. The occurrence of calyx yellowing or browning probably resulted from the breakdown of chlorophyll in response to ethylene, which was also observed by Bower et al. (2003), followed by leaf senescence.

The bruised area was evaluated in terms of two different defects: water soaking, in which damaged tissues were moist and translucent, and dry damaged area, in which there was dry and shrunken tissue. 'Radiance', followed by 'Cultivar A', had relatively more bruised fruit that developed water soaking, whereas 'Monterey' had more fruit with darker damaged areas than other cultivars.

Major defects observed in each cultivar in response to bruising were different. Decay, calyx yellowing/browning, and fruit with darker damaged areas were the major symp-

toms observed in 'Monterey'. For 'Radiance', decay, calyx yellowing/browning, and fruit with water soaking were the major symptoms, while 'Cultivar A' had more fruit with water soaking. Among all tested cultivars, Cultivar B exhibited the lowest bruising severity, whereas 'Monterey', 'Radiance', and 'Cultivar A' were more susceptible to bruising but responded with different symptoms. Saltveit (1997) described the first physical effects of wounding, which include removal of the protective epidermal layer, deposition of surface moisture (from the contents of broken cells), and exposure of the inner tissues to contaminants, including decay organisms. Water evaporation from the wound surface occurs later and the plant starts to respond physiologically to the wound. Surface water is first deposited and then lost as activation of healing proceeds. In this trial, most bruised fruit of 'Cultivar A' and 'Radiance' exhibited surface water in the damaged area where decay usually started. Other cultivars had more fruit with darker damaged areas where decay randomly spread. The healing processes activated after wounding among these cultivars were different and were presumably affected by the earlier wound response.

It would seem plausible that relative differences in wound ethylene production among strawberry cultivars may be, at least partly, a result of differences in the amount of damaged tissue resulting from the application of the same force. However, our results indicated that the cultivars with larger bruises (i.e., 'Cultivar A' and 'Monterey') had lower rates of wound ethylene production, suggesting that there are inherent genetic differences among these cultivars regarding wound ethylene production capacity.

In conclusion, bruising susceptibility varied among strawberry cultivars in terms of their responses, namely, respiration rate, ethylene production, and the phenotypic wound defects after being bruised. 'Monterey', 'Radiance', and 'Cultivar A' were more susceptible to bruising than 'Sweet Sensation' and 'Cultivar B', and they showed more ethylene-enhanced symptoms, including darker color or more severe water soaking at the injured area, or yellowing/browning of the calyx compared with unbruised CK fruit. 'Cultivar B', with the lowest ethylene production, also exhibited the lowest bruising severity, calyx yellowing/browning, and decay, whereas 'Radiance', with the highest ethylene production, exhibited the most severe bruise water soaking and among the most severe calyx yellowing/browning and decay.

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