Effect of Harvest Time and Fruit Firmness on Red Drupelet Reversion in Blackberry

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Abstract. Red drupelet reversion (RDR) is a postharvest disorder of blackberries (*Rubus* L. subgenus *Rubus* Watson) in which fully black drupelets revert to red after harvest. This disorder can negatively impact consumer perception of fresh-market blackberries. The cause of RDR is hypothesized to be related to intracellular damage sustained because of mechanical and environmental stress during and after harvest. Cultivars differ in susceptibility to this disorder; and cultural factors, including nitrogen rate, harvest and shipping practices, and climate during harvest, influence RDR severity. In this 2-year study, seven genotypes (cultivars and advanced selections) developed in the University of Arkansas System Division of Agriculture (UA) blackberry breeding program, with a range of fruit textures, were evaluated to determine whether firmness was correlated with RDR. In addition, fruit was harvested at four different times (7:00 AM, 10:00 AM, 1:00 PM, and 4:00 PM) to investigate whether harvest time influences RDR. All seven genotypes were harvested at the four times on two harvest dates per year and evaluated for RDR and firmness after 1 week of cold storage (5 °C). Fruit harvested early in the day had less RDR, with 7:00 AM harvests having the least RDR in both years. Significant genotypic differences in RDR and fruit firmness were found in each year. Firmness was negatively correlated with RDR in 2018 and 2019. These results indicate that growers may be able to reduce the prevalence of RDR by choosing cultivars with firm fruit texture and harvesting early in the day.

The global fresh-market blackberry industry has grown dramatically during the past few decades. From 2000 to 2010, the amount of blackberries shipped to domestic markets increased from 4500 to 54,545 kg (Clark and Finn, 2014). In 2018, the U.S. market for blackberries reached a value of over \$634 million in sales, with a 7.0% increase in market revenue, compared with sales in 2017 (California Strawberry Commission, 2018). The expansion of the fresh-market blackberry industry can be attributed to multiple causes. Newer cultivars have been released with improved characteristics that allow for long-distance shipping, extended harvest season, higher-quality fruit, and expanded production

area. Better production practices and postharvest handling have also helped decrease crop loss. Blackberries have many similarities to raspberries, which can allow raspberry growers to easily transition into the blackberry market. Blackberry plantings typically do not need to be replanted as often as raspberries and have lower disease pressure, which provides an economic incentive for growers. Additionally, consumer demand for blackberries has increased because of perceived health benefits associated with high levels of anthocyanins and antioxidants (Clark and Finn, 2011, 2014; Clark et al., 2007).

The continued expansion of the fresh-market blackberry industry is dependent on whether berries retain flavor and quality after harvest (Clark, 2016). Unfortunately, blackberries are one of the most perishable commodities because of their high respiration rates and fragile skin. Up to 40% of blackberry production is lost due to postharvest mishandling (Joo et al., 2011; Pritts and Handley, 1989). Red drupelet reversion (RDR) is a postharvest disorder of blackberries that occurs when black drupelets on ripe berries turn red during and after cold storage (Clark and Finn, 2011; Finn and Clark, 2012). Reverted drupelets typically have a more shriveled appearance upon closer inspection, with broken pistils surrounding the fruit, compared with fully black drupelets

(Edgley et al., 2019a). Whole shipments of blackberries can be rejected if over 10% of produce is not fully black or blue colored according to United States Department of Agriculture (USDA) marketing standards (USDA-AMS, 2016). Consumers tend to primarily base in-store purchases of blackberries on visual appearance such as uniform black color, glossiness, and freshness (Threlfall et al., 2016a, 2021). According to an online survey done by Threlfall et al. (2020), most consumers prefer larger, oblong-shaped berries, with 72.9% of the respondents preferring solid-black fruit with no reverted drupelets. When presented with three randomized clamshells filled with berries having varying levels of RDR, only 18.5% of consumers preferred the clamshell with the highest RDR in a consumer preference study conducted in person (Threlfall et al., 2021).

It has been speculated that RDR is caused by intracellular damage to the cell wall and vacuolar membranes that causes contents of the vacuole to spill out into the cytoplasm (Edgley et al., 2020). Tissue within reverted drupelets typically has larger intercellular spaces and ruptured cells indicative of widespread damage to the upper mesocarp (Salgado and Clark, 2016a). The vacuole can take up 90% of the cytoplasmic volume in a cell where it accumulates aromatics, anthocyanins, sugars, and tannins, which influence cellular development (Fontes et al., 2011). Edgley et al. (2019a) also used electrolytic leakage to measure damage to the plasma membrane of fruit tissue with significant increases from fully black drupelets (64.9%) to partially red (84.8%) and fully red drupelets (90.0%). The anthocyanins that are longer sequestered in the vacuole in damaged drupelets are susceptible to degradation, though different structural features of particular anthocyanins may affect their susceptibility to degradation (Edgley et al., 2019a, 2020).

Previous studies have investigated physiochemical changes in reverted drupelets and have found that the anthocyanin content is significantly lower in reverted drupelets compared with fully black drupelets (Edgley et al., 2019a; Kim et al., 2019). Kim et al. (2019) harvested berries from ‘Apache’, ‘Ouachita’, and ‘Triple Crown’ and observed a 39.1% to 43.4% decrease in total anthocyanin content in red drupelets after a week in cold storage. A 41.7% average decrease in cyanidin-3-glucoside, the dominant anthocyanin present in blackberries, was also found in all three cultivars (Kim et al., 2019). Edgley et al. (2019a) found a 58.2% decrease in total anthocyanins and a 59.7% average decrease in cyanidin-3-glucoside between black and red drupelets in a similar analysis performed with ‘Ouachita’ blackberries. This reduction in anthocyanins is suspected as the reason black drupelets turn red during storage (Edgley et al., 2019a, 2020).

Increasing fruit firmness is an important objective for fresh-market blackberry breeding programs. Fruit firmness is a quantitative trait that is typically evaluated after storage for postharvest retention (Clark and Finn, 2011). Perkins-Veazie et al. (1996) first observed an

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inverse relationship between fruit firmness and RDR using multiple genotypes (cultivars and advanced selections) after 7 d in cold storage (2 °C). Fruit firmness was partially dependent on cultivar, with the firmest genotype having the highest quality retention (Perkins-Veazie et al., 1996). The UA System blackberry breeding program has intensely selected for firm-fruited genotypes to increase postharvest storage capacity, which has led to the discovery of especially firm genotypes with a “crispy” texture. Salgado and Clark (2016a) compared four “crispy” genotypes and 11 standard-textured genotypes and showed that berry firmness was much higher and that 27.8% fewer berries were affected by RDR in the “crispy” genotypes compared with the standard-textured genotypes. Subsequent studies have compared the “crispy” breeding selection, A-2453, with other cultivars and have repeatedly shown that it has significantly lower rates of RDR, even after 1 to 2 weeks in cold storage (Felts et al., 2020; McCoy et al., 2016; Yin, 2017). Segantini et al. (2017) compared A-2453 with 10 other genotypes and found it had the lowest RDR (0.7%), highest firmness (9.6 N), and most uniform/glossy appearance. Consumer panels have also placed A-2453 as having the highest liking for berry color, which shows much promise for “crispy” selections (Threlfall et al., 2016a, 2016b).

The effects of cultural practices on RDR prevalence have been investigated. Excessive nitrogen fertilization increased bruise susceptibility of multiple species of fruit while decreasing fruit quality (Hussein et al., 2018; Lee and Kader, 2000; Mengel et al., 2001). ‘Ouachita’ blackberries had increased incidence and severity of RDR when fertilized with high levels of nitrogen (Edgley et al., 2018, 2019b). The methods of handling fruit during and after harvest can further influence RDR development (Perkins-Veazie et al., 1997). Up to 85% of ‘Ouachita’ berries that were hand-harvested following standard industry practices developed RDR, compared with only 6% of fruit that was harvested without handling, by cutting the pedicel above the fruit receptacle and placing the berries into cotton wool-lined cells (Edgley et al., 2019c). Edgley et al. (2019d) induced RDR in berries harvested without handling by exposing them to a point of impact injury. Over 95% of the fruit that was injured had some degree of color change, whereas the control samples not subject to injury had 5% RDR. Most of the color change occurred within 24 h of initial injury (Edgley et al., 2019d). Mechanical stress during shipping and transportation can be another factor contributing to RDR. Blackberries exposed to vibrations with a 10-Hz frequency and an amplitude of 0.5 g for 10 or 30 min had significantly more RDR after 2 d of storage at 3 °C than fruit that was not subjected to vibration (Pérez-Pérez et al., 2018).

Climate conditions before, during, and after harvest can also affect fruit quality and RDR. Fruit is softer and more susceptible to mechanical damage during and after harvest following a heavy rainfall (Clark and Finn, 2014; Finn and Clark, 2011). Proper

temperature management must be considered when storing berries after harvest (Bolda et al., 2012). Ideally, berries should instantly go through a cooling process after harvest to minimize heat exposure (Robbins and Moore, 1992). However, Edgley et al. (2019d) found that ‘Ouachita’ berries exposed to impact damage at warmer initial temperatures (>25 °C) before instantly cooling to 2 °C before a week in cold storage had increased rates of RDR, as opposed to berries that went through a more gradual cooling process. Salgado and Clark (2016b) also theorized that the rapid change of temperature could be a contributing factor leading to degradation of the tonoplast and cellular membrane fragmentation. These findings indicate that there may be an ideal rate of cooling after harvest for blackberries and that berries should be harvested with as much care as possible during cooler times of the day to minimize RDR (Edgley et al., 2019d). Lawrence and Melgar (2018) concluded that cultivar selection and environmental conditions at harvest impact how fruit will perform during postharvest.

Three separate single-year studies conducted in Clarksville, AR, by McCoy et al. (2016), Yin (2017), and Felts et al. (2020) have investigated whether harvesting blackberries at different times of day impacted rates of RDR. McCoy et al. (2016) found that harvesting at earlier times of day, especially before 10:00 AM, resulted in significantly lower RDR rates, and Yin (2017) also found that harvesting before noon significantly reduced RDR. Felts et al. (2020) compared RDR in nine genotypes harvested at 7:00 AM and 12:00 PM, but they found no significant impact of harvest time on RDR. However, the fact that fruit harvested at 7:00 AM was stored in an ice chest for 5 h longer than fruit harvested at 12:00 PM before sorting and placing the fruit in storage at 10 °C may have impacted those results. Edgley et al. (2019c) conducted another single-year study investigating the effect of temperature and harvest time on RDR in ‘Ouachita’ berries grown under a high tunnel in Tasmania. They observed lower rates of RDR when mean berry temperatures were below 23 °C, which was typically possible at 10:00 AM or before, when the ambient temperature was cooler during the peak of the Tasmanian blackberry season in Feb. 2016. The results of these studies suggest that in warm climates, berries harvested in the morning before the ambient air temperature increases may have less severe RDR.

A multiyear study is needed to further investigate the impact of harvest time on the development of RDR. Thus, the objective of this study was to evaluate the incidence of RDR in seven genotypes harvested at 7:00 AM, 10:00 AM, 1:00 PM, and 4:00 PM to determine whether harvest time and fruit firmness impact the rate of RDR in blackberries.

Materials and Methods

Plant material and cultural practices. The study was conducted at the UA System Fruit Research Station, Clarksville, in west-central Arkansas, lat. 35°31'5" N, long. 93°24'12"

W, U.S. Department of Agriculture (USDA) plant hardiness zone 7b (USDA, 2012). The soil type is Linker fine sandy loam (Typic Hapludults). The study ran in 2018 and 2019. Seven genotypes were harvested, including the following: A-2453, ‘Black Magic™’, ‘Natchez’, ‘Ouachita’, ‘Osage’, ‘Prime-Ark® 45’, and ‘Prime-Ark® Traveler’. Six of the seven genotypes in this study are commercial cultivars, whereas A-2453 is an advanced breeding selection that has been used in previous studies on “crispy” texture. These genotypes were chosen to represent a range of fruit firmness—from the soft home garden cultivar, Black Magic™, to the “crispy”-textured A-2453. Each genotype was harvested from a single 3.3-m plot containing five plants spaced 0.6 m apart.

Standard production practices were applied to all plots harvested for the experiment. The plots were drip irrigated as needed and fertilized regularly. Nitrogen fertilizer was annually applied early in the spring during budbreak in the form of ammonium nitrate (56 kg·ha⁻¹ N). A fertigation system applied 20N-4.4P-17K every 2 weeks, beginning at berry development until harvest. Liquid lime sulfur fungicide (94 L·ha⁻¹) was applied during budbreak for control of anthracnose [*Elsinoë veneta* (Burkh.) Jenkins]. Two additional fungicide applications, about 5 and 3 weeks before first harvest, were made to control anthracnose, botrytis fruit rot (*Botrytis cinerea* Pers.: Fr), and cane and leaf rust [*Kuehneola uredines* (Link) Arthur]. Multiple labeled insecticidal sprays containing zeta-cypermethrin, bifenthrin, and malathion were applied weekly for control of spotted wing drosophila (*Drosophila suzukii* Matsumura) starting at the beginning of berry development in late April until floriculture harvest in late June. An additional labeled insecticide containing bifenthrin was applied annually in October to control for raspberry crown borer (*Pennisetia marginata* Harris). The plants were trained to a four-wire, horizontal T-trellis system where the two lower wires were 0.5 m above the soil level and 0.5 m apart, while the upper two wires were about 1.0 m high and 0.8 m apart. Plants were pruned once floriculture harvest was complete in August and tipped at 1.1 m height in mid-May as the canes grew 8 to 15 cm above the trellis. Black plastic mulch at the base of the plants was used for weed control.

Harvest. The fruit was harvested on 14 and 19 June in 2018 and 18 and 27 June in 2019 at four times (7:00 AM, 10:00 AM, 1:00 PM, and 4:00 PM). Two replicate clamshells were collected at each harvest time. Fruit was harvested when the genotypes included in the study were in the early to midseason for harvest, and all harvested berries were at the shiny-black stage of development. Fruit harvested for the study were free of defects. The harvested fruit was placed inside 0.24-L vented clamshells (Form-Tex Plastics Corp., Houston, TX), with enough berries to fill the entire clamshell without any of the berries touching the lid. A filled clamshell represented a single replicate for each genotype from the same plot.

The fruit temperature was recorded using a Raytek Raynger ST IR crop temperature meter (Raytek Corp., Santa Cruz, CA) immediately following harvest. The temperature for each clamshell was calculated from an average of five measurements taken 15 to 17 cm from the berries in the clamshell. Harvested clamshells of fruit were then placed in vented cardboard flats within a portable cooler filled with ice packs until each harvest was finished. The clamshells were then placed in cold storage for 7 d at 5 °C.

Red drupelet reversion. After 7 d, the clamshells were removed from cold storage and allowed to return to room temperature (22 °C). The total number of berries in each clamshell was recorded before each berry was inspected for reverted drupelets. Moldy and diseased berries were discarded and not counted. Drupelets were considered reverted if they were red or maroon in color. Many of the reverted drupelets were shriveled or showed signs of leakage. Drupelets that had a dried up, shriveled appearance, but were not discolored, were assumed to be damaged by a pathogen and not counted as reverted. Following the protocol from Clark and Perkins-Veczie (2011), berries with three or more reverted drupelets were scored as reverted, while berries with two reverted drupelets or fewer were not counted as reverted. The number of reverted berries was divided by the total number of berries in each clamshell to calculate the percent reverted berries for each clamshell (replicate).

Firmness. Texture was measured on 10 randomly selected berries from each replicate following red drupelet assessment. Individual berries were placed on a platform horizontally where they were compressed using a Stable Micro Systems TA.XT.plus Texture Analyzer (Texture Technologies Corporation, Hamilton, MA) with a 5-kg load cell. A 7.6-cm diameter cylindrical and plane probe was used to compress each fruit 5 mm. Fruit firmness was measured in Newtons (N).

Composition. Three berries were selected at random from each clamshell, placed in labeled storage bags, and frozen (−10 °C) after postharvest evaluation for composition analysis. Each sample was analyzed to determine total soluble solids (SS) and titratable acidity (TA). The juice from each sample was extracted by thawing the berries and using cheesecloth to extract the juice. Soluble solids of the juice were measured using a Bausch & Lomb Abbe Mark II refractometer (Scientific Instrument, Keene, NH). Titratable acidity was measured by a Titroplus 862 compact titrosampler (Metrohm AG, Herisau, Switzerland) and prepared using 6 g of juice from each sample diluted with 50 mL of deionized, degassed water. A solute of 0.1 N sodium hydroxide was used as the titrant to an endpoint of pH 8.2 to measure the citric acid content. Soluble solids and TA were both expressed as percentages.

Drupelet diameter. Before composition analysis for samples in 2019, three berries in each storage bag were used to measure drupelet diameter. For each berry, five drupelets

were randomly selected to measure the diameter using digital calipers (Pittsburgh, Camarillo, CA). Drupelet diameter was measured without removing the individual drupelets from the berry, and an average value was calculated for all measurements per replicate.

Anthocyanins. High-performance liquid chromatography (HPLC) was performed for the 2019 samples using the remaining juice extracted from composition analysis. Samples from the four different harvest times that belonged to the same genotype and harvest date were combined for a total of 14 samples. Three milliliters of sample from each genotype per day were dried using a Speed Vac concentrator (Thermo-Savant, Holbrook, NY) and resuspended in 1 mL of 3% formic acid. The samples were then put through 0.45- μ m polytetrafluoroethylene (PTFE) syringe filters (Varian, Inc., Palo Alto, CA) before HPLC analysis. The analysis was performed based on previous methods (Cho et al., 2004). A Waters HPLC System (Waters Corporation, Milford, MA) was used that contained a 600 pump, a 717 Plus autosampler, and a 996-photodiode array detector. Separation was done using a 4.6-mm $\times$ 250-mm Symmetry (Waters Corporation, Milford, MA) C18 column with a 3.9-mm $\times$ 20-mm Symmetry C18 guard column. Anthocyanins (cyanidin-3-glucoside, cyanidin-3-rutinoside, cyanidin-3-xyloside, cyanidin-3-malonylglucoside, and cyanidin-3-dioxalylglucoside) were all quantified as cyanidin-3-glucoside equivalents (C3GE). Total monomeric anthocyanin results were expressed as mg C3GE/100 mL berry juice.

Statistical analysis. Data were analyzed as a three-way factorial with a completely randomized design using the GLIMMIX Procedure in SAS v. 9.4 (SAS Institute, Inc., Cary, NC). Clamshells served as the experimental units. Genotype, harvest time, year, and their respective interaction terms served as fixed effects, while the harvest date was nested within year as a random effect. Pooled anthocyanin data from 2019 was analyzed using the MIXED Procedure in SAS v. 9.4 (SAS Institute), with genotype as a fixed effect and harvest date as a random effect. Mean separation was performed with Tukey's honestly significant difference ($\alpha = 0.05$). Pearson's correlation coefficient was used to test the significance of the correlation between the severity of RDR and the firmness of each genotype.

Results

Climate conditions. The 2018 and 2019 growing seasons had different levels of precipitation and heat during blackberry harvest (Fig. 1). Total monthly rainfall was recorded between the months of April and June during each season. In 2018, monthly rainfall was 131 mm in April, 84 mm in May, and 71 mm in June. Rainfall in 2019 was much higher than in 2018; April had 164 mm, May had an especially heavy rainfall with 349 mm, and June had 207 mm of rain. During the first season of data collection in 2018, 0.8 mm of rain was recorded within 5 d before the first harvest date, while none was recorded for the second harvest date. During 2019, no rainfall

was recorded within 5 d of the first harvest date, but 113.5 mm of rain fell within 5 d before the second harvest date. Ambient air temperature was similar in both years (Fig. 1). The surface temperature of the fruit at harvest varied significantly depending on time of day in both years (Tables 1 and 2). In 2018 and 2019, the average berry temperature was lowest at 7:00 AM (22 to 25 °C), intermediate at 10:00 AM (29 to 32 °C), and highest at 1:00 PM (30 to 36 °C) and 4:00 PM (30 to 36 °C). Air temperature followed a similar pattern. In 2018, there was no difference in berry temperature or air temperature measured at 1:00 PM and 4:00 PM. However, air temperature was higher at 4:00 PM than 1:00 PM in 2019. Berry temperature and air temperature had strong positive correlations for both years ($r = 0.93$ and 0.87 , respectively).

Red drupelet reversion. Significant year $\times$ genotype interactions were found for many variables measured in this study, including RDR and firmness. Therefore, data for 2018 and 2019 are presented separately throughout the results. Overall, the severity of RDR was higher in 2019 than 2018. Rates of RDR differed significantly between harvest times for both years (Table 3). Later harvest times had higher rates of RDR, with each harvest time increasing in sequential order in 2018. The 1:00 PM harvest had the highest RDR rate in 2019 (30.28%). Although the 7:00 AM harvest had the lowest rate of RDR in 2019 (9.02%), it was not significantly different from the 4:00 PM harvest (15.37%).

The genotypic effect on RDR was also significant for both years. In 2018, A-2453, 'Osage', 'Ouachita', 'Prime-Ark[®] 45', and 'Prime-Ark[®] Traveler' had low rates of RDR between 1.42% to 5.20%. 'Natchez' (10.36%) and 'Black Magic[™]' (41.86%) had higher rates of RDR. All genotypes had a greater percentage of RDR during 2019; however, the difference in RDR between the first and second years were more pronounced in some genotypes than others. In 2019, A-2453 (3.30%) and 'Osage' (6.06%) had the lowest rates of RDR, while 'Prime-Ark[®] Traveler' (9.00%) and 'Ouachita' (9.29%) had intermediate RDR. 'Prime-Ark[®] 45' increased from 3.29% RDR in 2018 to 21.05% in 2019. 'Natchez' had 33.74% reverted berries in 2019, while 'Black Magic[™]' had the highest RDR of all genotypes at 79.83%. There was no significant harvest time $\times$ genotype interaction effect in either year for RDR. Air temperature and berry temperature were positively correlated with RDR in both years. Air temperature and RDR had a similar correlation in 2018 ($r = 0.24$) and 2019 ($r = 0.27$), while berry temperature was slightly less correlated with RDR in 2018 ($r = 0.22$) compared with 2019 ($r = 0.35$).

Firmness. There were no significant effects of harvest time or harvest time $\times$ genotype interaction on berry firmness in either year. Genotypes differed significantly in firmness for both years (Table 3). 'Black Magic[™]' was much less firm than the other six genotypes in both 2018 and 2019, measuring 2.78 N and 2.27 N, respectively. A-2453 was firmer than all other genotypes in both years (13.92 N in

Fig. 1. Monthly rainfall and ambient air temperature at the University of Arkansas System Division of Agriculture Fruit Research Station, Clarksville, AR (2018 and 2019).

2018 and 10.71 N in 2019), and ‘Prime-Ark® Traveler’ was the second-firmest genotype in both years. ‘Natchez’, ‘Osage’, ‘Ouachita’, and ‘Prime-Ark® 45’ had intermediate firmness both years. Fruit firmness ratings for all genotypes in 2019 were lower than 2018. Berry firmness and RDR were negatively correlated in 2018 ($r = -0.53$) and 2019 ($r = -0.36$) (Fig. 2).

Composition. There were no significant effects for harvest time when evaluating SS

and TA in 2018 or 2019. A significant harvest time $\times$ genotype interaction was found for TA in 2019. Data for TA was pooled given the F statistic for genotype ($F = 20$) was an order of magnitude greater than the F statistic for the harvest time $\times$ genotype interaction effect ($F = 2.03$) (data not shown). Our composition data indicates that fruit was within commercially acceptable ranges, and that fruit collected at different harvest times was at the same relative level of maturity.

Soluble solids varied significantly among genotypes in each year, though overall SS was higher in 2018 than 2019. ‘Ouachita’ had the highest SS in 2018 (15.12%) and 2019 (12.33%), respectively, with statistically similar levels in ‘Prime-Ark® 45’ (11.63%), ‘Osage’ (11.41%), and ‘Black Magic™’ (11.21%) in 2019. SS was negatively correlated with RDR in 2019 ($r = -0.21$), but no correlation was

detected between SS and RDR in 2018. There were significant genotypic differences for TA in both years. ‘Black Magic™’ and ‘Natchez’ had the highest levels of TA (0.81%, 0.78%, respectively) in 2018, and ‘Black Magic™’ had significantly higher TA than any other genotype in 2019 (0.88%). The genotypes with the lowest TA in 2018 included ‘Prime-Ark® Traveler’, A-2453, and ‘Ouachita’; and in 2019, ‘Prime-Ark® Traveler’, A-2453, ‘Prime-Ark® 45’, and ‘Osage’ were in the lowest acidity group. Berry reversion was positively correlated to TA in 2018 ($r = 0.38$) and 2019 ($r = 0.46$).

Drupelet diameter. The diameter of individual drupelets measured in 2019 varied across genotypes and harvest times, but no significant harvest time $\times$ genotype interaction effect was found. A-2453 (5.45 mm) and ‘Ouachita’ (5.34 mm) had the highest average drupelet diameter, and ‘Black Magic™’ had the lowest (4.49 mm). Berries harvested later in the day had smaller drupelet diameters, with an average length of 4.90 mm at 1:00 PM and 4:00 PM, compared with drupelet diameters measuring 5.17 mm and 5.15 mm at 7:00 AM and 10:00 AM, respectively. Drupelet diameter was negatively correlated with RDR and positively correlated with firmness in 2019 ($r = -0.58$ and 0.40, respectively).

Anthocyanins. Total anthocyanins of the juice ranged from 22.95 to 74.85 mg/100 mL but did not differ among genotypes (Table 4). Cyanidin-3-glucoside was the dominant anthocyanin in all genotypes and ranged from 17.60 to 66.65 mg/100 mL in ‘Black Magic™’ and ‘Natchez’, respectively. Cyanidin-3-rutinoside was the only individual anthocyanin that varied significantly among genotypes. However, no statistical differences among treatment means were detected using Tukey’s honestly significant difference (Table 4). No correlation was found between the level of cyanidin-3-rutinoside and RDR. ‘Osage’ had 5.85 mg/100 mL

Table 1. Air temperature and fruit surface temperature of seven blackberry genotypes measured during each harvest time, Clarksville, AR (2018 and 2019).

Yr	Harvest date	Harvest time	Air temp ^z (°C)	Fruit surface temp ^y (°C)
2018	14 June	7:00 AM	26.11	25.45
	14 June	10:00 AM	31.67	31.98
	14 June	1:00 PM	35.00	35.91
	14 June	4:00 PM	34.44	36.19
	19 June	7:00 AM	25.00	22.35
2019	19 June	10:00 AM	29.44	29.07
	19 June	1:00 PM	30.56	30.03
	19 June	4:00 PM	31.11	30.36
	18 June	7:00 AM	23.33	21.50
	18 June	10:00 AM	28.33	29.67
	18 June	1:00 PM	30.00	32.67
	18 June	4:00 PM	32.22	31.11
	27 June	7:00 AM	25.00	24.58
	27 June	10:00 AM	30.00	30.41
	27 June	1:00 PM	31.67	33.80
	27 June	4:00 PM	32.78	34.05

^zAir temperature measured at each harvest time per harvest date.

^yAverage fruit surface temperature of seven genotypes collected at each harvest time per harvest date, each genotype had two replicate clamshells harvested, with five berries per clamshell, measured directly after harvest.

Table 2. Main effect means for harvest time for fruit surface temperature of seven blackberry genotypes, Clarksville, AR (2018 and 2019).

Effect	2018		2019	
	Air temp ^z (°C)	Fruit surface temp ^y (°C)	Air temp (°C)	Fruit surface temp (°C)
Harvest time				
7:00 AM	25.56 a ^x	23.83 a	24.15 a	22.96 a
10:00 AM	30.54 b	30.48 b	29.15 b	30.02 b
1:00 PM	32.71 c	32.81 c	30.82 c	33.21 c
4:00 PM	32.73 c	33.14 c	32.50 d	32.54 c
P value	<0.0001	<0.0001	<0.0001	<0.0001

^zAverage air temperature measured at each harvest time.

^yAverage fruit surface temperature at each harvest time.

^xMeans with different letter(s) are significantly different ($\alpha = 0.05$) using Tukey’s honestly significant difference.

Table 3. Main and interaction effect means for harvest times and seven blackberry genotypes for firmness, red drupelet reversion, soluble solids, titratable acidity, and drupelet diameter, Clarksville, AR (2018, 2019).

Effects	2018				2019				
	Red drupelets (%)	Firmness (N)	Soluble solids (%)	Titratable acidity (%)	Red drupelets (%)	Firmness (N)	Soluble solids (%)	Titratable acidity (%)	Drupelet diameter (mm)
Harvest Time									
7:00 AM	2.67 b	7.25 a ^z	13.52 a	0.58 a	9.02 c	4.90 a	11.07 a	0.59 a	5.17 a
10:00 AM	3.94 b	6.97 a	12.89 a	0.63 a	16.47 b	5.12 a	11.01 a	0.51 a	5.15 a
1:00 PM	5.00 ab	7.12 a	13.40 a	0.59 a	30.28 a	5.06 a	11.23 a	0.57 a	4.90 b
4:00 PM	8.99 a	7.59 a	13.33 a	0.63 a	15.37 bc	5.39 a	11.06 a	0.56 a	4.90 b
P value	0.0003	0.1855	0.1595	0.5357	<0.0001	0.2799	0.8809	0.2233	<0.0001
Genotype									
A-2453	1.42 c	13.92 a	12.82 bc	0.57 cd	3.30 d	10.71 a	10.72 bcd	0.45 cd	5.45 a
Black Magic™	41.86 a	2.78 e	13.65 b	0.81 a	79.83 a	2.27 e	11.21 abcd	0.88 a	4.49 d
Natchez	10.36 b	8.35 bc	13.05 bc	0.78 ab	33.74 b	5.04 cd	10.30 cd	0.67 b	4.94 c
Osage	1.44 c	6.61 d	13.50 b	0.60 bc	6.06 cd	4.36 cd	11.41 abc	0.54 bcd	4.85 c
Ouachita	2.09 c	6.05 d	15.12 a	0.55 cd	9.29 c	4.20 d	12.33 a	0.59 bc	5.34 ab
Prime-Ark® 45	3.29 c	8.22 c	12.73 bc	0.61 bc	21.05 b	5.20 c	11.63 ab	0.44 d	5.12 bc
Prime-Ark® Traveler	5.20 bc	9.72 b	12.25 c	0.42 d	9.00 c	7.84 b	10.18 d	0.45 cd	5.08 bc
P value	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Harvest time × genotype (P value)	0.2161	0.7756	0.1319	0.5418	0.0873	0.7853	0.2874	0.0160	0.1213

^zMeans with different letter(s) are significantly different ($\alpha = 0.05$) using Tukey's honestly significant difference.

cyanidin-3-rutinoside, while 'Ouachita' had only 0.25 mg/100 mL, and 'Prime-Ark® Traveler' had no measurable cyanidin-3-rutinoside. Cyanidin-3-malonylglucoside ranged from 0.85 to 1.80 mg/100 mL, and cyanidin-3-dioxalylglucoside levels ranged from 0 to 2.85 mg/100 mL.

Discussion

Environmental effects on RDR. Significant main effects for genotype and harvest time on RDR were observed in both years of the study, with no significant interaction between these factors. SS and TA were within commercially acceptable ranges for all genotypes and harvest times. There were no differences

in the firmness, SS, or TA of berries harvested at 7:00 AM, 10:00 AM, 1:00 PM, and 4:00 PM in either year, indicating that berries harvested at different times were equally ripe and that time of harvest did not impact any of these variables. Berries harvested at 7:00 AM had the lowest RDR at 2.67% in 2018 and 9.02% in 2019. The highest RDR rates occurred in fruit harvested at 1:00 PM and 4:00 PM. This finding agrees with the results of McCoy et al. (2016), Yin (2017), and Edgley et al. (2019c), who found RDR sharply increased for harvests at 10:00 AM or later.

Temperature changes are suggested to play a major role in influencing RDR severity at different harvest times (Edgley et al., 2019c; McCoy et al., 2016; Yin, 2017). In

this study, average air temperature increased throughout the day, with the greatest change occurring between 7:00 AM and 10:00 AM. Yin (2017) and McCoy et al. (2016) observed similar weather patterns in their research, which was also conducted at the UA System Fruit Research Station. Yin (2017) found that air and berry temperature increased sharply between 7:00 AM and 12:00 PM before leveling out from 12:00 PM to 4:00 PM. McCoy et al. (2016) also found a 6.1 °C increase in air temperature between harvests at 7:00 AM and 10:00 AM, with no significant difference in temperatures during later harvest times. In this study, average air temperature started out 1.0 to 1.5 °C higher than average berry temperature at 7:00 AM before converging at 10:00

Fig. 2. Pearson's correlation coefficient for red drupelet reversion and firmness of blackberry genotypes, harvested from the University of Arkansas System Division of Agriculture Fruit Research Station, Clarksville, AR (2018 and 2019). Hollow marker on a solid line indicates 2018 data. Solid marker on a dotted line indicates 2019 data.

Table 4. Main effect means of anthocyanins for seven blackberry genotypes, Clarksville, AR (2019)^z.

Genotype	Cyanidin-3-glucoside (mg/100 mL)	Cyanidin-3-rutinoside (mg/100 mL)	Cyanidin-3-xyloside (mg/100 mL)	Cyanidin-3-malonylglucoside (mg/100 mL)	Cyanidin-3-dioxyglucoside (mg/100 mL)	Total anthocyanins (mg/100 mL)
A-2453	24.3	1.05	0.95	0.85	0.80	28.20
Black Magic™	17.60	2.85	1.05	0.80	0.65	22.95
Natchez	66.65	3.30	0.45	1.50	2.85	74.85
Osage	33.85	5.85	0.30	1.10	0.90	42.10
Ouachita	44.65	0.25	1.80	1.80	1.05	49.55
Prime-Ark® 45	22.05	4.20	0.50	1.30	0.00	28.15
Prime-Ark® Traveler	24.50	0.00	0.70	0.75	1.15	27.20
<i>P</i> value	0.1573	0.0434	0.5161	0.7020	0.0842	0.1667

^zNo genotypic differences ($\alpha = 0.05$) were found for any attribute using Tukey's honestly significant difference.

AM. From 1:00 PM onwards, average berry temperature was like the air temperature. Previous research indicated that 'Arapaho' blackberries maintained equal g_s in temperatures ranging from 20 to 35 °C (Stafne et al., 2001), which may allow blackberry plants to maintain relatively stable canopy temperatures even in very warm conditions. Edgley et al. (2019c) also found that fruit temperature increased more than air temperature during the day in a study of blackberries grown in a high tunnel in Tasmania, and they attributed this effect to solar activity warming the fruit. The low correlation between temperature and RDR might be caused by different environmental or canopy conditions producing a confounding effect at each harvest.

Lawrence and Melgar (2018) suggested that other factors (such as relative humidity, plant water status, and harvest date) could also influence RDR severity. Precipitation particularly affected results in this study. Rainfall was greater during harvest in 2019 and likely impacted firmness, RDR, and SS content. Firmness and SS content were lower, while RDR rates were much higher in 2019. The 113.5 mm of rain that fell 5 d before the second harvest in 2019 may have affected the quality of berries collected that day. Heavy rainfall has been linked to decreased fruit firmness, and growers are advised to postpone harvest for 4 d after significant rain events (Perkins-Veazie and Clark, 2005). McCoy et al. (2016) and Salgado and Clark (2016a) both reported that a wetter harvest season had negative impacts on overall fruit firmness. A future study looking into the firmness and RDR rate of berries grown in a high tunnel or rainout shelter with different overhead irrigation rates applied shortly before harvest may be useful to determine the effects of rainfall on RDR and develop harvest recommendations for growers.

Genotypic differences in RDR. Significant genotypic differences in RDR were observed in both years of this study, and berry firmness and RDR were negatively correlated in 2018 ($r = -0.53$) and 2019 ($r = -0.36$). 'Black Magic™' was significantly less firm than all other genotypes and had the highest RDR in both 2018 and 2019. McCoy et al. (2016) also found that 'Black Magic™' was the least firm and had the highest RDR of all cultivars and genotypes tested. 'Black Magic™' is a home-garden cultivar that is not recommended for long-term shipping as it has

repeatedly had poor postharvest performance (Clark et al., 2014). The "crispy" selection A-2453 performed as expected, with significantly higher firmness than all other genotypes in the trial. A-2453 was among the group of genotypes with the lowest RDR in each year, as other researchers have shown (Felts et al., 2020; McCoy et al., 2016; Salgado and Clark, 2016a, 2016b, 2016c; Segantini et al., 2017; Yin, 2017).

Firmness gradually decreases during the ripening phase of physiological maturity for multiple fruit crops as the polysaccharide components of the primary cell wall and the middle lamella begin to degrade to reduce intercellular adhesion (Brummell, 2006). Soft blackberries have a higher susceptibility to bruising and cellular damage, leading to increased RDR. Fortunately, breeders have selected for blackberry genotypes that retain firmness during ripening (Clark, 2005). The relationship between fruit firmness and RDR has been documented in previous studies (Felts et al., 2020; McCoy et al., 2016; Perkins-Veazie et al., 1996; Salgado and Clark, 2016a, 2016b; Segantini et al., 2017; Yin, 2017). Ripe berries from the "crispy" breeding selection, A-2453, had much greater cell-cell adhesion, thicker cell walls, and more uniform cellular structure than the standard-textured cultivar 'Natchez' (Salgado and Clark, 2016a, 2016b). A-2453 also had the least weight loss of all other genotypes during storage (Yin, 2017). In addition, Segantini et al. (2017) evaluated multiple blackberry genotypes for postharvest storage potential and found that weight loss was negatively correlated to firmness ($r = -0.68$). The increased integrity of cellular membranes and reduced weight loss in storage of firmer genotypes likely protect them from some of the cellular damage and bruising that causes RDR.

Other factors may also contribute to genotypic differences in RDR. In fact, only 28.4% and 12.7% of the genotypic variation in RDR was explained by firmness in 2018 and 2019, respectively. 'Osage' and 'Ouachita' had lower RDR in both years than anticipated based on berry firmness. While A-2453 was over twice as firm as 'Osage' and 'Ouachita' in both years, RDR levels for 'Osage' and 'Ouachita' in 2018 were not significantly different from A-2453; and 'Osage' was also not significantly different from A-2453 in 2019. McCoy et al. (2016) also found that 'Osage' had the second lowest rate of RDR after

A-2453. On the other hand, 'Natchez' had the second highest level of RDR after 'Black Magic™' but was significantly firmer than 'Osage' and 'Ouachita' in both years. 'Osage' was previously reported as slightly firmer than 'Natchez' upon release (Clark, 2013). One explanation for this inconsistency is that other confounding variables influence RDR levels in addition to firmness. Environmental conditions such as precipitation likely affect firmness because of its quantitative nature (Clark, 2005; Salgado and Clark, 2016a).

Titrateable acidity was correlated with RDR in both years, and SS was negatively correlated with RDR in 2019. 'Black Magic™' and 'Natchez' had the highest TA and RDR in both years. It is possible that the higher acidity of these cultivars was a result of the intercellular damage that caused RDR (Fontes et al., 2011; Salgado and Clark, 2016a). Edgley et al. (2019a) found no differences in TA, but a lower pH between fully reverted drupelets and fully black drupelets. A reduction in pH below 3 will cause anthocyanins to shift to their red flavylium ion in isolated conditions and affect the color of purified solutions (Castañeda-Ovando et al., 2009). However, given the high concentration of anthocyanins in blackberries and their copigmentation with other polyphenols, it is unlikely that low pH results in the drastic color change seen in reverted drupelets (Edgley et al., 2019a). Blackberry genotypes vary widely in their acidity (Clark, 2005), and this correlation between RDR and TA is likely an artifact of the small number of genotypes selected for this study.

Genotypes with larger drupelets tended to have less RDR in 2019. A-2453 and 'Ouachita' had the largest drupelet diameter of the genotypes in this study, while 'Black Magic™' had the smallest diameter. The larger drupelet diameters of A-2453 and 'Ouachita' may be related to increased turgor pressure and cellular membrane integrity resulting from varying cuticle properties or respiration rates specific to each genotype (Hertog et al., 2004; Yin, 2017). Average drupelet diameter across genotypes decreased later in the day when air and berry temperatures were the highest. Transpiration rates are expected to increase as the plants are exposed to more sunlight and heat during the day. As transpiration rates increase, water leaves the cell and the elastic modulus decreases (Hertog et al., 2004; Johnston et al., 2001; Yin, 2017). Higher transpiration and water loss might contribute to the smaller drupelet

diameter of berries harvested at 1:00 PM and 4:00 PM, compared with the morning harvests and higher rates of RDR at these harvest times.

However, drupelet diameter was only measured for the 2019 harvest season, and the observed negative correlation between RDR and drupelet diameter could be an artifact of the small number of genotypes used. Although overall fruit size and weight were not measured, A-2453 was previously shown to be smaller and lighter than the other blackberry cultivars in this study while Natchez was the largest and the heaviest (Felts et al., 2020; Threlfall et al., 2016a, 2016b). The negative relationship between drupelet diameter and fruit size might be the result of resource allocation, as smaller fruit may have a denser cellular structure (Ali, 2012). The positive correlation found between drupelet diameter and firmness supports this suggestion. Smaller fruit with fewer drupelets were also reported to experience less RDR than larger berries in a study conducted with ‘Ouachita’ (Edgley et al., 2018, 2019b). Similarly, smaller peach [*Prunus persica* (L.) Batsch] and apple (*Malus domestica* Borkh.) cultivars were reported to have less impact damage during harvest resulting in less bruising (Ericsson and Tahir, 1996; Maness et al., 1992). A multiyear study with a larger set of genotypes is needed to further examine the relationship among RDR, drupelet diameter, and fruit size.

The anthocyanin content and composition of different genotypes may also impact their susceptibility to RDR. Edgley et al. (2019a) and Kim et al. (2019) both found significant reductions in total anthocyanins in red drupelets compared with black drupelets. Anthocyanins vary in their stability depending on the sugars and other functional groups attached to the anthocyanidin (Welch et al., 2008), and cyanidin-3-glucoside is suspected to encounter the most chemical changes during color reversion as polymeric anthocyanin derivatives are created (Pérez-Pérez et al., 2018). Edgley et al. (2019a) found that cyanidin-3-rutinoside and two of the acylated anthocyanins [cyanidin-3-dioxyalylglucoside and cyanidin-3-(6''-malonylglucoside)] detected in ‘Ouachita’ blackberries were not significantly reduced in red drupelets compared with black drupelets, suggesting that these compounds may be somewhat protected from degradation during RDR.

In this study, juice samples were combined from the four harvest times, and individual anthocyanins were measured in these pooled samples during the 2019 season to investigate whether differences in anthocyanin composition among the tested genotypes could explain any of the observed variation in RDR. Total anthocyanin levels did not vary between genotypes, and cyanidin-3-glucoside was the most common anthocyanin found for all the samples, representing 77% to 90% of the anthocyanins measured. Cyanidin-3-rutinoside was the only anthocyanin found to vary between genotypes, though none of the genotypes were significantly different from each other according to Tukey’s honestly significant difference. Edgley et al. (2019a) suggested that the disaccharide sugar compounds in cyanidin-3-

rutinoside could inhibit nucleophilic cleavage and preserve the anthocyanin during reversion. Cyanidin-3-rutinoside was also shown to have better stability during thermal treatment at 95 °C and storage than other anthocyanins in black currant (*Ribes nigrum* L.) (Rubinskiene et al., 2005). While no significant correlation was found between cyanidin-3-rutinoside content and RDR in this study, the relatively high cyanidin-3-rutinoside content of ‘Osage’ (13.7% of total anthocyanins) might contribute to its lower than anticipated RDR rates given its relatively low firmness. Kim et al. (2019) also found genotypic differences in cyanidin-3-rutinoside among ‘Apache’, ‘Ouachita’, and ‘Triple Crown’. Thus, it may be possible to breed for increased cyanidin-3-rutinoside content, among other beneficial compounds, in blackberry (Cho et al., 2004). The anthocyanin data were collected for only one season with only two replicates per sample. Future multiyear studies should evaluate the anthocyanin composition of a wider selection of blackberry genotypes in reverted and nonreverted drupelets to determine whether selection for cultivars with increased concentration of acylated and disaccharide anthocyanins could reduce the severity of RDR.

Conclusion

The results of this study add further support to the relationship between fruit firmness and RDR, which was documented in previous studies. The “crispy” genotype, A-2453, had the lowest RDR of the genotypes evaluated, while the soft-fruited home-garden cultivar, Black Magic™, had the highest RDR in both years. Other factors, including acidity, drupelet diameter, and composition of anthocyanins with greater stability than cyanidin-3-glucoside may also contribute to genotypic differences in susceptibility to RDR. However, future research with a greater number of genotypes is needed to determine the potential effect of these factors on RDR. As previously reported by McCoy et al. (2016) and Yin (2017), berries harvested earlier in the day had significantly less RDR after a week in cold storage. RDR rates were lowest for the 7:00 AM harvest, when average air and berry temperatures were lowest, signifying that cooler temperatures during harvest have a positive effect on fruit quality. Other environmental factors, including precipitation, likely also affected RDR and fruit firmness in this study. Our results indicate that growers may be able to reduce the severity of RDR by choosing cultivars with firm fruit texture and harvesting early in the morning.

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