Photosynthetic Light Response of Floricane Leaves of Erect Blackberry Cultivars from Fruit Development into the Postharvest Period

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Abstract. The photosynthetic light response of commercial blackberry cultivars (*Rubus* L. subgenus *Rubus* Watson) is largely unexplored, although they are frequently grown in full sun. In this experiment, light response curves of floricanes leaves from the cultivars Natchez, Apache, Navaho, and Von were examined throughout the following production stages: before shiny black fruit were present (before harvest, BH), during peak production of fruit (peak harvest, PH), and when most fruit had fallen from plants or any remaining were dull black (after harvest, AH). Each cultivar was evaluated between an irradiance of 2000 and 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The estimated maximum photosynthetic rate (photosynthetic capacity, P_{Nmax}) was greater BH than AH across all cultivars, whereas ‘Natchez’ had a greater P_{Nmax} BH and PH compared with the other cultivars. During AH, all cultivars had a similar P_{Nmax} . The BH response curves declined under the highest irradiance measured, whereas the PH and AH response curves remained stable at similarly high irradiance. Of the four cultivars, Apache, Navaho, and Von appeared to be more photosynthetically limited than Natchez under increasing irradiance. Based on the cultivar-specific performance observed, blackberry response to light is a relevant trait that breeding programs should consider for improving cultivar adaptability to local and regional conditions.

Blackberry (*Rubus* subgenus *Rubus* Watson) production has greatly increased since 2005 in North America, Central America, Australia, and Europe as a result of newly developed floricanefruiting and primocane-fruited cultivars from both university and private breeding programs, development of marketing outlets, and an increase in fresh-market consumption (Clark and Finn, 2014; Hall, 2017). Numerous breeding efforts have improved fruit flavor, size, and shelf life, and there is a continued interest in improv-

ing plant traits, such as a greater tolerance to cold temperatures during flowering and tolerance to intense sunlight (Clark and Finn, 2008; Takeda et al., 2013). With regard to light, *Rubus* spp. exhibit plasticity with respect to architecture and leaf physiology under different levels of irradiance (Gallagher et al., 2015). Field plantings are often designed to achieve maximum light interception depending on the latitude of production (Pritts and Hanson, 2017), although high irradiance combined with high temperature is known to lead to fruit sunscald, leaf burn, an increase in the incidence of white drupelet disorder (Finn and Clark, 2017; Takeda et al., 2013), and occasionally total plant collapse (Finn and Clark, 2011). Furthermore, the interception of light beyond the maximum capacity of the photosystems or photoprotective measures of the plant may induce oxidative stress before visible damage (Mullineaux and Karpinski, 2002). High irradiance is known to cause excess excitation energy in the light harvesting systems and reduce the efficiency of photosystem II (Barber, 1995; Powles, 1984). To counter light stress and prevent damage, plants use redox signaling and signal transduction pathways to elicit photoprotective measures and acclimate to persistent high light conditions (Foyer et al., 2017; Matsubara et al., 2016), but relatively little information exists on the performance of cultivated *Rubus* spp. under contrasting sunlight irradiance in warm subtropical growing regions.

Studies comparing blackberry production in full and partial sunlight show that plants receiving high irradiance have more concentrated flowering and harvest periods than plants with reduced irradiance (Gallagher et al., 2015; Rotundo et al., 1998). High tunnels are often used to extend the growing season for *Rubus* spp. in cooler climates, whereas plastic films can be formulated to buffer temperatures and alter the transmission of light to improve fruit yield and quality (Heidenreich et al., 2012; Strik et al., 2007). In warmer production regions, shade netting has recently been explored to reduce plant heat stress and possibly white drupelet disorder on blackberries (Caillouet, 2016; Spiers et al., 2014; Stafne et al., 2017). Similarly, rotating shift-arm trellises have shown to protect fruit from intense sunlight and high temperatures (Takeda et al., 2013). Despite several options to reduce or modify natural irradiance, the vast majority of production occurs without protective overhead structures such as high tunnels or shade nets (Strik et al., 2007).

Currently, a greater understanding of cultivar-specific responses to increasing irradiance is needed to avoid reduced photosynthetic capacity caused by high irradiance, and possibly warrant shade or tunnel structures for sun protection of some cultivars over others. Indeed, a comparison of several blackberry cultivars in South America concluded that the light compensation point and net photosynthesis varied between the four cultivars studied (Enciso and Gómez, 2004), but little is known about the photosynthetic performance of common commercial, field-grown blackberries and how they respond to irradiance during the growing season. We hypothesized that the plant photosynthetic response to light is cultivar specific and may also change with the stages of fruit development. Therefore, the objective of this work was to determine the photosynthetic capacity of four common commercial erect blackberries by comparing their responses to increasing irradiance.

Materials and Methods

Plant material and study design. The research was performed in a former variety trial of 5-year-old blackberry plants located at the Musser Fruit Research Center of Clemson University in Seneca, SC (lat. 34°36'22"N, long. 82°52'39"W), during 2019. Three plots consisting of five plants each of the erect blackberry cultivars Apache, Natchez, Navaho, and Von were used, being part of the variety trial with a randomized complete block design. Cultural management followed regional commercial practices: in-row white plastic mulch as orchard floor management, drip irrigation (each plant received 3.4 L·h⁻¹, 3 h per week), and fertigation with liquid calcium nitrate (applied once a week between April and July, and once a month in August and September) for an annual amount of nitrogen of 22.4 kg·ha⁻¹. Fruit was not harvested at regular

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intervals during the season to maintain fruit on the measured plants.

Sampling periods, weather parameters, and light response curves. The photosynthetic light responses of the four cultivars were determined between the months of May and July during three sampling periods: 1) BH, 2) during PH, and 3) when nearly all or all fruit had naturally fallen from the plants (AH). The BH sampling period was determined by the time in which plants had only green or red developing fruit and few to no shiny black fruit present, the PH sampling period was designated by the weeks when many shiny black fruit were present and few developing fruit remained, and the AH sampling period was when plants had few dull black or no fruit remaining, with the majority of fruit removed by natural abscission. Weather and environmental parameters were monitored using a Davis Instruments Vantage Pro weather station (Davis Instruments, Hayward, CA). The daily maximum total solar irradiance along with the mean total solar irradiance at 0830 HR and 1200 HR were similar throughout the study period, with the highest and lowest levels recorded in June after a multiday rain event (Fig. 1). Daily precipitation was nearly absent during the last 2 weeks of May, but was more common in June and July. Mean daily humidity ranged between 61% to 77% in May, 53% to 96% in June, and 61% to 86% in July. Mean daily temperatures ranged from 23.9 to 27.6 °C in May, 20.2 to 27.5 °C in June, and 23.4 to 28.9 °C in July. Light response curves were determined using a LICOR 6400-XTR portable photosynthesis system (LI-COR, Lincoln, NE) with an auxiliary LICOR 6400-02B light-emitting diode light source between 0830 HR and 1200 HR. For each cultivar, measurements were taken from fully developed, east-facing floricanes on the third or fourth node of fruiting laterals 0.5 to 1.5 m off the ground. In the case of AH measurements, measurements were made on floricanes with visible pedicels after fruit abscission. Light response and gas exchange were measured for each photosynthetic photon flux density (PPFD) fraction of 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, starting from the highest irradiance at 2400 to 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and then at 100, 50, and 0 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (for a detailed plotting of the curve in the area near the compensation point) at 2-min average intervals (Evans and Santiago, 2014; Lobo et al., 2013). Light response curves for BH and PH were carried out using one leaf per plant and four plants per cultivar, whereas AH light response curves were constructed using one leaf per plant from only two plants per cultivar as a result of time constraints. Therefore, for each sampling period, the mean of four plants from the available 15 plants across the three plots were used to construct light response curves per cultivar during BH and PH, whereas two plants were used during AH. The same leaves were used for each set of measurements on a given day, measuring one cultivar or alternating between two cultivars for a total of four leaves each morning: ‘Apache’ (21 May; 22 May; 17 June; 2 July; 8 July), ‘Natchez’ (21 May; 22 May; 17 June; 2 July; 29 July), ‘Navaho’ (29 May; 4 June; 3 July; 9 July; 29 July), and ‘Von’ (28 May; 3 June; 3 July; 16 July; 30 July).

8 July), ‘Natchez’ (21 May; 22 May; 17 June; 2 July; 29 July), ‘Navaho’ (29 May; 4 June; 3 July; 9 July; 29 July), and ‘Von’ (28 May; 3 June; 3 July; 16 July; 30 July).

As a follow-up study to better understand the influence of fruit presence during BH on light response, the same methods were used to analyze both ‘Natchez’ and ‘Apache’ leaves the following season. However, 1 week before measuring light response, all developing fruit were removed from half of the plants, and the light response from four plants with and without fruit was compared for each cultivar.

Data and statistical analysis. Individual photosynthetic response curves were constructed using mean measurements per plant at each light level (SigmaPlot 13.0; Systat Software, San Jose, CA) using a modified rectangular hyperbola equation (Eq. [1]) described by Ye (2007), which resulted in the lowest sum of the squares of the errors among other equations commonly used to calculate light response curves as suggested by Lobo et al. (2013).

$$P_N = \Phi(I_{0, \text{comp}}) \times \left[\frac{(1 - \beta \times I)/(1 + \gamma \times I)}{(I - I_{\text{comp}})} \right] \quad [1]$$

Variables in the equation include net CO_2 assimilation (P_N), the quantum yield [$\Phi(I_{0, \text{comp}})$] within the range of when irradiance equals zero and the light compensation point (I_{comp}), the PPFD or irradiance (I), and several adjusting coefficients (β and γ) inde-

pendent of the irradiance (Ye, 2007). The P_N , $P_{N_{\text{max}}}$, mitochondrial respiration rate (R_D), light compensation point (I_{comp}), and saturation irradiance (I_{max}) were calculated using Ye’s (2007) equation model provided by Lobo et al. (2013). Comparisons of photosynthetic parameters by sampling period or cultivar were done using analysis of variance and Student’s least significant difference mean separation tests using JMP® (version 14.1.0; SAS Institute, Cary, NC).

Results and Discussion

The photosynthetic light response of blackberry plants depended on the stage of fruit development and cultivar (Fig. 2, Table 1). Across all cultivars, the response curves of BH fruit had greater $P_{N_{\text{max}}}$ values ($P \leq 0.05$) than AH. The response curves for BH showed declining P_N values under increasing irradiance, with ‘Navaho’ reaching its $P_{N_{\text{max}}}$ at the lowest irradiance among all cultivars (661 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), whereas $P_{N_{\text{max}}}$ started to decline near 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for ‘Apache’ and ‘Von’, and at 1125 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for ‘Natchez’. Among the cultivars studied, ‘Natchez’ had greater $P_{N_{\text{max}}}$ values than the other three cultivars BH and at PH, whereas ‘Navaho’ had the lowest values; however, $P_{N_{\text{max}}}$ was similar among all cultivars AH.

The P_N values at PH or AH did not decline with increasing irradiance, with the exception of the PH curve of ‘Natchez’, which decreased slightly starting at an irradiance of more than 1600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Fig. 1. Weather parameters during the 2019 growing season, including mean solar irradiance at 0830 HR and 1200 HR (filled and open triangles respectively), and the daily maximum (dotted line) (A); the daily maximum (solid line), minimum (dotted line), and mean humidity (open circles, %), along with rainfall (cm, gray bars) (B); and the maximum (solid line), minimum (dotted line), and mean temperature (filled circles, °C) during the study, along with arrows denoting sampling periods of before harvest (BH), peak harvest (PH), and after harvest (AH) by cultivar: ‘Apache’ (Ap; 21 May; 22 May; 17 June; 2 July; 8 July), ‘Natchez’ (Nz; 21 May; 22 May; 17 June; 2 July; 29 July), ‘Navaho’ (Nh; 29 May; 4 June; 3 July; 9 July; 29 July), and ‘Von’ (V; 28 May; 3 June; 3 July; 16 July; 30 July) (C).

Table 1. Photosynthetic parameters of four commercial blackberry cultivars (Apache, Natchez, Navaho, and Von) during three sampling periods (before harvest, peak harvest, and after harvest). Parameters include maximum photosynthesis (P_{Nmax}), dark respiration (R_D), light compensation point (I_{comp}), and light saturation point (I_{max}).

Cultivar	Sample period	Parameter ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			
		P_{Nmax}	R_D	I_{comp}	I_{max}
Apache	Before	12.2 B ² a ³	2.1 A a	33.1 A a	1005 AB a
	Peak	9.2 B a	1.9 AB a	35.6 A a	1194 A a
	After	10.3 A a	1.9 A a	32.4 AB a	1261 A a
Natchez	Before	15.2 A b	2.1 A a	35.4 A b	1125 A a
	Peak	18.1 A a	2.7 A a	45.3 A b	1345 A a
	After	9.9 A c	2.2 A a	63.5 A a	1613 A a
Navaho	Before	8.7 C a	1.3 B a	18.6 B b	661 B b
	Peak	9.6 B a	1.1 AB a	15.9 A b	1040 A a
	After	6.8 A a	1.1 A a	31.8 AB a	1076 AB a
Von	Before	11.3 BC a	0.4 B b	15.4 B a	998 A ab
	Peak	9.4 B b	0.9 B ab	17.9 A a	1216 A a
	After	7.5 A b	1.5 A a	20.2 B a	774 B b

²Uppercase letters show significant differences between cultivars by sampling period according to Student's least significant difference (LSD) mean separation tests ($\alpha = 0.05$).

³Lowercase letters show significant differences between sample periods by cultivar according to Student's LSD mean separation tests ($\alpha = 0.05$).

Fig. 2. Mean CO_2 assimilation (P_N , $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) by increasing irradiance (photosynthetic photon flux density, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of four commercial blackberry cultivars (Apache, Natchez, Navaho, and Von) during before harvest (solid circles), peak harvest (open circles), and after harvest (solid triangles) sampling periods. Error bars represent $\pm$ SE (before and peak harvest, $n = 4$; after harvest, $n = 2$).

Regarding P_{Nmax} , 'Natchez' had notably greater values BH ($P \leq 0.01$) and PH ($P \leq 0.001$), but not AH ($P > 0.05$) in comparison with the other three cultivars. When comparing sampling periods by cultivar, 'Natchez' was estimated to have a greater ($P \leq 0.001$) P_{Nmax} BH and at PH than AH. 'Von' was

similar and had a greater P_{Nmax} ($P \leq 0.05$) BH than at PH or AH.

It is well known that the development and persistence of fruit has been shown to increase or maintain the demand of assimilates, and therefore P_N , as seen with raspberry (*Rubus idaeus* L.) and apple leaves (*Malus domestica* Borkh.) (Cameron et al., 1993; Naschitz et al., 2014). 'Natchez' is known for its large fruit size (Clark and Moore, 2008), and during the three previous years in the variety trial, 'Natchez' had larger fruit size than 'Navaho' and 'Von', but was comparable to 'Apache' (Lawrence et al., 2020). Factors such as the absence of fruit acting as photosynthetic sinks or leaf age have been found to explain the reduction of P_N during AH in other species (Fernandez and Pritts, 1994; Tartachnyk and Blanke, 2004). This reduction and that of P_{Nmax} during AH was not consistent among cultivars, and genotypic differences may best explain the cultivar-specific responses to light, as it seems to occur for adaptability to high temperatures (Stafne et al., 2001). To elucidate the influence of the presence of fruit on the high P_{Nmax} values of 'Natchez', light response curves of plants with and without fruit were performed the following growing season. 'Natchez' plants had similar P_{Nmax} in plants with and without fruit (19.2 and $19.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). There were no differences in 'Apache' plants with and without fruit either (17.4 and $15.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), and values of 'Natchez' were greater ($P \leq 0.01$) than those of 'Apache' (data not shown). Thus, the influence of a strong photosynthetic sink, in this case fruit presence BH, did not explain why 'Natchez' had greater P_{Nmax} values in comparison with the other cultivars. Another simultaneous sink of photosynthates was the growth of primocanes, previously identified as a strong sink in raspberry (Fernandez and Pritts, 1994). Although growth measurements were not taken, there were no visual differences in primocane appearances among cultivars, further supporting a hypothesis that light re-

sponse curves may be specific to cultivar, similar to the results reported by Enciso and Gómez (2004) on four Colombian blackberry cultivars.

'Natchez' had greater R_D values in comparison with the other three cultivars analyzed across sampling periods ($P \leq 0.01$; Table 1). By cultivar, R_D values were similar among sampling periods except for 'Von', which showed lower R_D ($P \leq 0.05$) BH than AH. The acclimation of R_D to available light has been explored in forest species (Lusk and Reich, 2000) and generally decreases with more shaded environments. Because all cultivars were grown in the field under similar irradiance, the greater R_D values of 'Apache' and 'Natchez' BH in comparison with 'Navaho' and 'Von' is perhaps a reflection of larger fruit size or yield, as all cultivars had similar R_D values AH. Nonetheless, the brief study that occurred the following growing season examining both 'Apache' and 'Natchez' plants with and without fruit showed no differences in R_D , I_{comp} , or I_{max} BH (data not shown). Yield among the four cultivars had been calculated the previous 3 years and revealed all four cultivars had similar yield, with the exception of 'Apache' the final year of the variety trial (Lawrence et al., 2020); however, no yield data were collected for this study. Therefore, it is possible differences in fruit yield among the four cultivars may have resulted in different R_D values as well.

Across sampling periods, 'Natchez' had the greatest I_{comp} ($P \leq 0.001$) values in comparison with the other three cultivars (Table 1). The I_{comp} values for 'Natchez' and 'Navaho' BH and PH were both less ($P \leq 0.05$) than AH, whereas 'Apache' and 'Von' had similar I_{comp} values for all three sampling periods. The I_{comp} values for each of our cultivars were similar to previous reports of 'Illini Hardy' blackberries, which—under 100% irradiance—had an I_{comp} value of $40 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Gallagher et al., 2015). Only 'Natchez' and 'Navaho' appeared to have an increase in I_{comp} after fruit removal. Although a decrease of I_{max} has been observed in apple leaves after fruit removal, I_{comp} is not always affected by the presence of fruit (Tartachnyk and Blanke, 2004). Because the increase in I_{comp} for 'Natchez' and 'Navaho' AH was not the result of an increase in R_D , it is possibly an artifact of older leaves being analyzed.

The I_{max} value of 'Navaho' BH was less than that at PH or AH ($P \leq 0.01$), whereas 'Von' had a lower I_{max} value AH compared with PH ($P \leq 0.05$; Table 1). 'Apache' and 'Natchez' showed numerically increasing I_{max} values from BH throughout AH, although differences were not significant. Light saturation of blackberries has been previously reported to occur at 750 to 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Caillouet, 2016), which could be between one third to one fourth the maximum daily irradiance of most blackberry growing regions, depending on latitude (about a third of the maximum irradiance at our location; Fig. 1). Light saturation in this study appeared to be generally greater than the

Fig. 3. Mean ratio of mesophyll CO_2 concentration to atmospheric CO_2 concentration (C_i/C_a) by increasing irradiance (photosynthetic photon flux density, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of four commercial blackberry cultivars (Apache, Natchez, Navaho, and Von) during before harvest (solid circles), peak harvest (open circles), and after harvest (solid triangles) sampling periods. Error bars represent $\pm$ SE (before and peak harvest, $n = 4$; after harvest, $n = 2$).

values reported by Caillouet (2016), and several cultivars, including Apache and Natchez, had estimates of I_{max} greater than $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for each sample period.

The C_i/C_a of the BH sampling period showed increasing values for all cultivars when receiving irradiance greater than 1600 to $1800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ BH (Fig. 3). The PH and AH sampling periods, however, showed more consistent C_i/C_a values during increasing irradiance (with the exception of PH and AH 'Apache', and AH 'Von'). The mean C_i/C_a between the irradiance values of 600 and $1600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ revealed that all cultivars were similar during the BH period ($P > 0.05$), 'Apache' and 'Navaho' had a lower C_i/C_a value than 'Natchez' and 'Von' PH ($P \leq 0.001$), and 'Von' had lower values than 'Apache', 'Natchez', and 'Navaho' AH ($P \leq 0.001$). Similar analysis of stomatal conductance across the same values showed that 'Natchez' had greater conductance than other cultivars BH and at PH (data not shown).

To our knowledge, we present the first information regarding C_i/C_a curves by different irradiance for commercial blackberry cultivars. Studying how C_i/C_a is influenced by irradiance can provide responses indirectly on the performance of Rubisco (increasing C_i/C_a values may correspond with

an accumulation of CO_2 in the mesophyll and indicate reduced Rubisco activity). BH blackberry leaves showed increasing C_i/C_a values under light conditions greater than $1800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Yet, the C_i/C_a value did not increase with irradiance during PH or AH. Thus, it is possible that the leaves became acclimated to high irradiance as the growing season progressed, in comparison with BH leaves. The process of leaf acclimation has been documented before in *Arabidopsis* (Matsubara et al., 2016), and such photoprotective measures under greater irradiance seem plausible because the decrease of C_i/C_a at high irradiance was primarily observed on BH leaves.

The production of blackberries in warmer climates faces the challenge of achieving the required chilling hours (Clark and Finn, 2008) while maintaining floral competence and fruit quality when temperatures and solar irradiation are high (Makus, 2010; Stanton et al., 2007). Cultural practices of planting in a north-south orientation, along with rotating shift-arm trellises, may reduce the amount of direct sunlight within the orchard (Takeda et al., 2013), but production areas for blackberries exist in regions that often receive both high irradiance and high temperatures during production, and support plants with simpler

trellis structures. The use of reflective mulches, high tunnels, and shade structures in warmer climates (Caillouet, 2016; Makus, 2010; Rotundo et al., 1998) has been suggested to alter irradiance and reduce temperature, but some of these strategies may not be appropriate for all growers, depending on latitude or orchard orientation.

This study demonstrates there are cultivar-specific differences that may affect blackberry performance in the field. Specifically, the four commercial blackberry cultivars studied had different responses to increasing irradiance. 'Natchez', which had greater BH and PH $P_{N\text{max}}$ values, may perform best in regions that receive greater irradiance, whereas cultivars such as 'Navaho', which had lower $P_{N\text{max}}$ values throughout the sample periods, may adapt better to areas with lower irradiance. Provided the demand of fresh-market blackberry fruit continues, evaluations of cultivars by photosynthetic performance in warmer climates could assist breeders or growers when making selections for heat- or light-tolerant genotypes, depending on climatic field conditions.

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