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Low-Temperature Survival of Flower Buds of Nine Blackberry Cultivars

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Abstract

Commonly-grown blackberry cultivars are susceptible to low-temperature injury throughout their dormant period in the midwestern United States. A study was conducted to evaluate the temperature at which 50% of the flower buds of nine blackberry cultivars were killed (T_{50}) following exposure to low temperatures at three selected times during dormancy. Blackberry cultivars evaluated included 'Apache', 'Arapaho', 'Caddo', 'Osage', 'Ouachita', 'Navaho', 'Natchez', 'Ponca', and 'Von'. Tissue for artificial freezing tests was collected from a research planting near New Franklin, MO on 17 Jan, 28 Feb, 21 Nov 2022, and 11 Jan and 18 Nov 2023. Immediately after each collection, canes were prepared for low-temperature exposure at a cooling rate of 3 °C/h. Primary flower bud hardiness among all cultivars varied by 7.2, 13.6, and 6.8 °C in Jan, Feb and Nov 2022 sampling dates, respectively. Due to a naturally occurring low-temperature event (-22 °C) in Dec 2022, canes were collected and primary flower bud survival without artificial freezing was evaluated on 11 Jan and 28 Feb in 2023. 'Natchez' primary buds had the highest T_{50} values and low percent survival among the cultivars. In Jan and Feb 2022, T_{50} values of 'Natchez' secondary buds were 7 and 11 °C lower than its primary buds, respectively. At all test dates, 'Ouachita' primary buds had consistently low T_{50} values (-21.7 °C in Jan 2022) or relatively high percent survival compared with other cultivars.

Cultivation of blackberry (*Rubus* L. subgenus *Rubus* Watson) as a horticultural crop in the United States (US) began in the early 1800s (Darrow 1915). By 1851, wild selections, such as 'Dorchester', 'Lawton', and 'Snyder' blackberry plants were marketed for their fruit productivity and quality, but only the latter cultivar was considered winter hardy in the northeastern US (Hedrick 1922). For winter protection, cold-sensitive blackberry canes were typically bent to the ground and covered with soil or organic mulches (Hansen 1907).

By 1909, there were about 140 named blackberry introductions with plantings reported in 48 states (Darrow 1915). Early efforts with blackberry at agricultural experiment stations in the northern US were focused on the evaluation of introductions for fruit yield, flavor, and firmness, disease resistance, and low-temperature survival of plants (Darrow 1915; Hansen and Harlson 1907; Hedrick 1922; Paddock 1896). Although H. Ness at College Station, Texas, and W.H. Lawrence, and J.L. Stahl at Puyallup, Washington began breeding blackberries for various traits in 1908 and 1909, respectively, G.L. Slate and R. Wellington focused on breeding for cold hardiness at the New York State Agricultural Experiment Station at Geneva in 1912 (Darrow, 1937). In 1915, cultivars, such as 'Blowers', 'Ancient Briton', 'Eldorado', 'Merseuau', 'Snyder' and 'Taylor' tolerated temperatures as low as -34 °C and were considered hardy by Darrow (1915).

Since the early 20th century, considerable

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progress in the adaptation of blackberry to short production cycles, intensive production systems, and mechanical harvest, as well as the development of thornless, primocane-fruiting, low-chilling (≤ 300 h) cultivars has been achieved via public and private breeding (Clark et al. 2007; Moore 1984). However, crop loss due to low-temperature injury remains a limiting factor in blackberry production not only in the US but also worldwide (Danek and Kolodziejczak 1993; Gruner and Kornilov 2020; Finn and Strik 2015; McWhirt and Clark 2021; Stanisavljevic 1999).

By the latter 20th century, research efforts in several states (Arkansas, Maryland, Missouri, Oregon, and West Virginia) focused on the low-temperature survival of blackberry flower buds, blossoms, and canes (Hummer et al. 1995; Kraut et al. 1986; Moore and Brown 1971; Warmund et al. 1986, 1992). Moore and Brown (1971) reported that thorny cultivars, such as 'Darrow' and 'Hedrick' had lower injury ratings than 'Dallas', 'Humble', 'Brazos', and 'Wells Beauty' when evaluated after a record low-temperature period in January in Arkansas. 'Dirksen' canes were more cold-tolerant than 'Smoothstem' thornless blackberry canes following a natural cold event occurring in late winter in Silver Spring, Maryland (Kraut et al. 1986). Due to the unpredictability of low-temperature events, Warmund et al. (1986) used controlled-freezing tests in the laboratory to compare the low-temperature survival of early cultivar releases from the Arkansas Agricultural Experiment Station breeding program ['Cherokee', 'Comanche', 'Cheyenne', Shawnee', A-1172 ('Navaho')] with 'Darrow' as a standard of comparison. In this study, 'Darrow' primary flower buds had greater low-temperature survival at -34 °C than those of other cultivars, except 'Comanche'. In a later study conducted in Corvallis, Oregon, flower buds of 41 blackberry cultivars were subjected to controlled freezing in the laboratory after tissue collection in January and storage at -2 °C for 27 d. 'Dirksen', and 'Eldorado' had the lowest T_{50} values (-25 and -22 °C, respectively), while 'Bedford Giant', 'Santiam', and 'Zielinski' T_{50} values were the highest (-9 °C) among the cultivars tested (Hummer et al. 1995).

In most laboratory evaluations of blackberry hardiness, primary flower buds were evaluated due to their earlier differentiation of reproductive organs (Hummer et al. 1995; Warmund et al. 1986, 1988, 1989, 1993). Although the prevalence of reproductive secondary flower buds and their degree of floral organ differentiation varies among blackberry cultivars, these tissues generally survive lower temperatures than those of primary buds (Warmund and George 1990). The evaluation of individual floral primordia mortality is tedious and comparisons between cultivars are difficult due to the varying numbers of low-temperature exotherms across a range of temperatures (Warmund and George 1990). Also, highly sensitive sensors are needed for the detection of low-temperature exotherms, which are associated with intracellular freezing and floral primordia injury.

In addition to studies evaluating the winter hardiness of buds and canes of blackberry cultivars, various strategies have been tested to protect sensitive plants from low-temperature injury, including the use of spun-bonded rowcovers and the culture of plants in high tunnels or other structures (Bushway et al. 2008; Demchak 2009; Hatterman-Valenti, 2016; Mettler and Takeda et al. 2008; Takeda and Phillips 2011). Although fruit was harvested from 'Triple Crown' blackberry plants grown in high tunnels for multiple years in New York, they failed to produce berries when outdoor temperatures fell below -17 °C on 19 dates with two episodes of rapidly falling temperatures (Pritts 2015). In other trials with low-temperature sensitive cultivars, blackberry canes and floral tissues were protected from mid-winter and spring frost injury when plants were trained to a rotating cross-arm trellis and placed under a rowcover ($165 g \cdot m^{-2}$) (Takeda et al. 2013).

While research has been conducted on the low-temperature survival of older blackberry cultivars, flower bud hardiness of more recently released cultivars has not been assessed in controlled experiments without the use of rowcover or protective structures. Thus, the objective of this study was to evaluate the primary bud hardiness of nine, thornless floricane-fruiting blackberry cultivars grown in the open field and sampled at selected dates during dormancy.

Materials and Methods

A blackberry trial was planted at the University of Missouri Horticulture and Agroforestry Research Center, New Franklin, MO (lat. 39.017251°N, long. -92.737408°W, elevation 196 m) on 29 May 2020. Tissue-cultured plants of 'Apache', 'Arapaho', 'Caddo', 'Natchez', 'Navaho', 'Osage', 'Ponca', 'Ouachita', and 'Von' were spaced at 0.9 m x 2.4 m and trained on a V trellis with three plants of each cultivar in each of ten replications arranged in a randomized complete block design. Fertilization, irrigation, and pest management followed local guidelines (Beckerman et al. 2022; Warmund 2022).

Meteorological data were recorded using an environmental monitoring system (U30; Onset, Bourne, MA) located 2 m from the blackberry planting. The temperature sensor (S-TMB-M006; Onset, Bourne, MA) and precipitation sensor (S-RGB-M002) collected data at 10 s intervals, which were averaged and recorded at 10 min intervals to obtain daily minimum and maximum temperatures.

Tissue for the freezing tests was collected on 17 Jan, 28 Feb, and 21 Nov 2022 and 11 Jan and 18 Nov 2023. Sampling dates were selected to assess flower bud hardiness during mid-winter, just before bud swell in late winter, and in the fall as buds were acclimating to low temperatures. For freezing tests at each sampling date, tissue was collected from all plants per plot in each replication of the planting. Seven cuttings, consisting of three nodes each, were collected from the middle portion of one-year-old lateral canes at approximately 1 m above the soil surface.

Immediately after samples were collected, a cutting from each cultivar was placed in moist cheesecloth and wrapped in aluminum foil for each of seven test temperatures, including an unfrozen control. A 0.01-mm-diameter copper-constantan thermocouple was placed in contact with a flower bud of one sample of each test temperature to monitor tissue temperature and thermocouple output was read with a digital thermometer (Omega Engineering, Stamford, CT). Samples were then placed in a programmable freezer (Tenney Benchmaster; Tenney Engineering, Union, NJ) at -2 °C for one hour before cooling at 3 °C/h. The cheesecloth froze and seeded the tissue with ice at about -1 °C. Samples were removed from the freezer at 3 °C intervals, using a range of temperatures (-12 to -33 °C) likely to produce tissue injury (Warmund et al. 1992). After removal from the freezing chamber, samples were thawed at 4 °C for 24 h and placed at 21 °C for 5 d before floral bud evaluation. Unfrozen controls were maintained at 4 °C during the freezing test and then transferred to 21 °C at the same time as samples exposed to subfreezing temperatures were placed at the latter temperature. To assess floral bud survival, 3 primary flower buds per cutting and any secondary buds present at nodes were sectioned with a razor blade and examined for oxidative browning under a dissecting microscope at 40X magnification. The numbers of injured and uninjured floral primordia were recorded and the modified Spearman-Karber equation was used to calculate T_{50} values for buds at each sampling date (Bittenbender and Howell, 1974). For statistical analyses, T_{50} values for each collection date were subjected to an analysis of variance using PROC GLIMMIX. Means were separated using Fisher's protected least significant test ($P \leq 0.05$).

Due to low winter temperatures (-22 °C) at the research center on 22 and 23 Dec 2022, additional samples were collected to assess flower bud injury without exposure to a laboratory freezing test on 11 Jan and 28 Feb 2023. Six cuttings each with 5 flower buds were collected in a similar manner as described above from each of five replications of each cultivar. Samples were sealed in bags and placed at 21

°C for 5 d before assessment of bud mortality. The odds (i.e., probability) of bud survival as a proportion of the total number of buds examined were calculated and the GLMMIX procedure with a link = logit function for a binomial distribution was used for data analysis. Odds were calculated from the antilog of the logit value and back-transformed [% bud survival = odds/(1 + odds)] for the presentation of the data. Means were separated as described above.

Results

Air temperatures. New Franklin MO is within USDA Plant Hardiness Zone 6b, which has average extreme minimum temperatures ranging from -20.6 to -17.8 °C (US Department of Agriculture, Agricultural Research Service 2023). The lowest air temperature of the 2021-2022 dormant period (-17 °C) was recorded on 21 Jan and subsequent minimum daily air temperatures were relatively cold, ranging from 6 to -15 °C until the 28 Feb sampling date in 2022 (Fig. 1). The lowest daily temperature recorded in the autumn preceding the 21 Nov 2022 test was -8 °C. Total precipitation in the 2-week periods before the Jan, Feb, and Nov 2022 tests was 9.9, 14.0, and 9.4 mm, respectively.

On 22 and 23 Dec 2022, the lowest daily minimum air temperature for the 2021-2023 dormant period was recorded (-22 °C) (Fig. 2). Jan 2023 was relatively warm with daily minimum temperatures ranging from -13 to 7 °C. Minimum temperatures in early February were as low as -13 °C, but the day before sampling, the minimum temperature was 6 °C. The lowest daily temperature recorded in the autumn preceding the Nov 2023 test was -5 °C on the first day of the month but thereafter the minimum daily temperature only fell below freezing (-1 °C) on 17 Nov 2023. Total precipitation in the 2-week periods before the Jan and Feb 2023 tests was 10.4 and 41.4 mm,

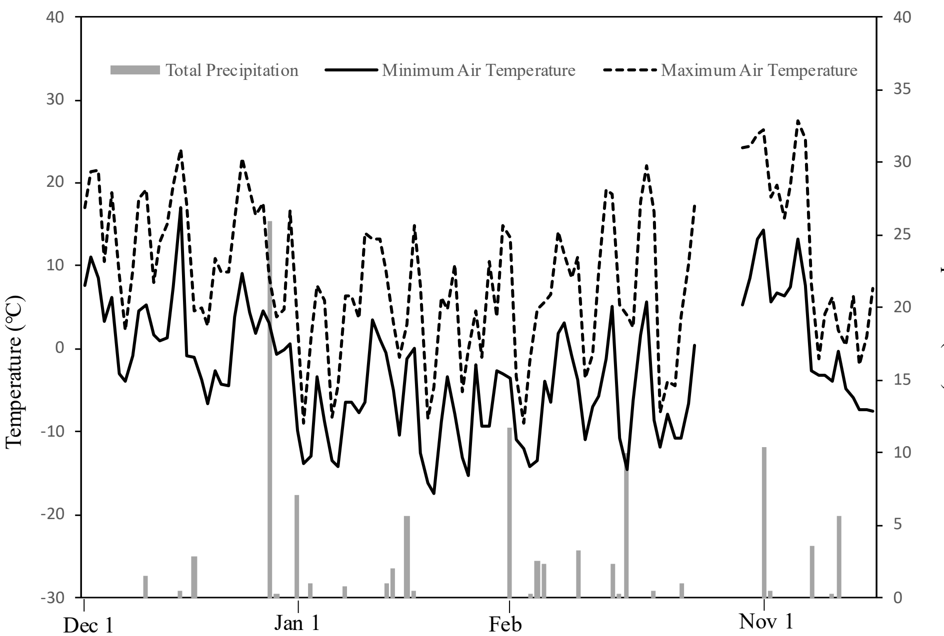

Fig. 1. Total precipitation, and minimum and maximum daily air temperatures in Dec 2021 to Feb 2022 and Nov 2022.

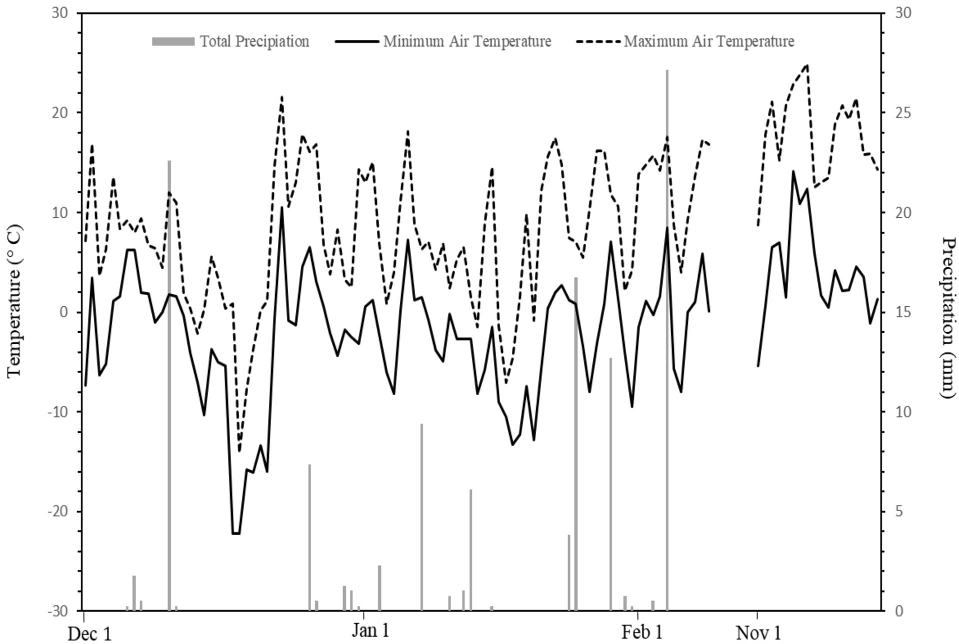

Fig. 2. Total precipitation, and minimum and maximum daily air temperatures in Dec 2022 to Feb 2023 and Nov 2023.

respectively. No precipitation was recorded from 1 to 18 Nov 2023.

Primary flower bud cold hardiness in 2022. In Jan 2022, primary flower bud T_{50} values among cultivars ranged from -21.7 for 'Ouachita' to -14.5 °C for 'Natchez' (Table 1). 'Von', 'Arapaho', 'Osage', 'Apache' and 'Navaho' had similar T_{50} values, which were also lower than those of 'Ponca', 'Caddo', and 'Natchez'.

By 28 Feb 2022, flower bud T_{50} values for most cultivars were ≤ 2.2 °C higher than the values from the January test (Table 1). However, 'Osage', 'Ponca', and 'Natchez' T_{50} values were considerably higher (2.8 to 6.8 °C) in February compared with those in January. 'Ouachita' had the lowest T_{50} value and 'Natchez' had the highest value in Feb 2022.

In Nov 2022, T_{50} values for 'Ouachita', 'Von', and 'Apache' were lower than those of 'Osage', 'Ponca', 'Caddo', and 'Natchez' (Table 1). Although there was less discrimination among cultivars when buds were acclimating to low temperatures in autumn, 'Natchez' was considerably more susceptible to injury than all other cultivars.

Primary flower bud cold hardiness in 2023. Due to the low-temperature event in Dec 2022, more than 50% of the unfrozen control primary buds were injured when evaluated in Jan 2023, which precluded the calculation of T_{50} values. However, some primary flower buds of 'Ouachita', 'Von', and 'Navaho' survived following exposure to -24 °C during the laboratory freezing test. When primary buds were examined without artificial freezing in January, 'Ouachita', 'Von', and 'Navaho' had the highest percent survival (46.0, 39.3, and 38.7, respectively), and 'Natchez' had the lowest percent survival (4.7) (Table 2).

By the Feb 2023 collection date, little or no additional low-temperature injury occurred (Table 2). Results were nearly similar to those in January with survival as follows: 'Ouachita'

> ‘Von’ and ‘Navaho’ > ‘Caddo’ > ‘Arapaho’ > ‘Ponca’, ‘Osage’ and ‘Apache’, > ‘Natchez’.

In Nov 2023, ‘Ouachita’ had the lowest T_{50} values for primary buds when freezing tests were conducted (Table 3). ‘Von’, ‘Apache’, and ‘Navaho’ T_{50} values were 1.4 to 2.0 °C higher than that of ‘Ouachita’. Primary buds of ‘Osage’ and ‘Ponca’ were more susceptible to low-temperature injury than all other cultivars except for ‘Natchez’.

Secondary flower bud cold hardiness. When buds were examined following the freezing test, most cultivars had very few or no secondary buds present at nodes. Due to the low numbers of secondary buds of most cultivars, T_{50} values for most cultivars could not be calculated for each sampling date. In contrast, reproductive secondary buds were present at every node of ‘Natchez’. In Jan, Feb, and Nov 2022, T_{50} values of ‘Natchez’ secondary buds were -21.7, -18.5, and -15.8 °C , respectively, In Jan and Feb 2023, 34% of the secondary buds survived the natural freezing conditions in the field at each sampling date. In Nov 2023, 33, 40, and 67% of ‘Natchez’ secondary buds exhibited injury at -12, -15, and -18 °C, respectively, with a calculated T_{50} value of -17.1 °C.

Discussion

Floricane-fruiting blackberry cultivars evaluated in this study varied in primary bud survival following exposure to low temperatures. At November sampling dates, primary buds of ‘Von’, ‘Apache’, and ‘Navaho’ had similar T_{50} values and had similar or slightly higher T_{50} values as ‘Ouachita’ buds in 2022 and 2023, respectively, indicating that these cultivars had acclimated to lower temperatures than most others included in these evaluations (Tables 1, 3).

Except for ‘Navaho’, T_{50} values of primary buds of nearly all cultivars were generally lower in January than in February. However, T_{50} values of ‘Ouachita’ and ‘Von’ primary buds only increased by ≤ 0.4 °C by late Febru-

Table 1. Mean T_{50} values of primary flower buds of nine blackberry cultivars grown at New Franklin, MO at selected dates in 2022.

	T_{50} value (°C)		
Cultivar	17 Jan	28 Feb	21 Nov
Ouachita	-21.7 a [i]	-21.3 a	-18.9 a
Von	-19.9 b	-19.7 b	-18.5 a
Arapaho	-19.7 b	-18.3 c	-17.9 abc
Osage	-19.5 b	-15.3 d	-16.9 cd
Apache	-19.3 b	-18.5 c	-18.5 a
Navaho	-19.1 b	-19.3 bc	-18.1 ab
Ponca	-17.5 c	-14.7 d	-16.1 d
Caddo	-17.3 c	-15.1 d	-17.1 bcd
Natchez	-14.5 d	- 7.7 e	-12.1 e

[i] Means represent 5 replications of each 3-node cutting for each cultivar. LS-means within columns followed by common letters do not differ at the 5% level of significance by Fisher’s protected LSD test.

Table 2. Percent survival of flower primordia in primary buds of nine blackberry cultivars grown at New Franklin, MO at selected dates in 2023.

Cultivar	11 Jan	28 Feb
Ouachita	46.0 a [i]	43.3 a
Von	39.3 b	34.0 b
Arapaho	16.7 d	20.7 d
Osage	12.7 e	14.0 ef
Apache	15.3 de	11.3 f
Navaho	38.7 b	36.0 b
Ponca	17.3 d	15.3 e
Caddo	22.7 c	24.7 c
Natchez	4.7 f	4.0 g

[i] Means represent 5 replications of each 3-node cutting for each cultivar. PROC GLIMMIX using a link = logit function for binomial distributions was used to analyze percent survival of flower primordia in buds as a proportion of the total number of buds examined. Back transformed data [% survival of flower primordia in buds = odds/(1+ odds)] are presented. LS- means within columns followed by common letters do not differ at the 5% level of significance by Fisher's protected LSD test.

ary (Table 1). In contrast, T_{50} values of 'Osage' and 'Natchez' primary buds increased by 4.2 and 6.8 °C, indicating that these cultivars deacclimated with a substantial loss of bud hardiness from mid- to late winter.

Also in January and February, 'Ouachita' primary buds had the lowest T_{50} values (Table 1) and the highest primary bud survival (Table 2). 'Von' and 'Navaho primary buds were slightly less cold-tolerant than those of 'Ouachita' at January and February test dates. The similarities in T_{50} values and percent bud survival of 'Von' and 'Navaho' buds at all test dates are likely due to their parentage. 'Von' originated from an F_1 seedling population of 'Navaho' x NC 194, which may contribute to its low-temperature tolerance (Fernandez et al. 2013).

In this study, the T_{50} value for primary reproductive 'Navaho' buds collected in Jan 2022 was similar (-19.1 °C) to that reported in Jan 1988 in an earlier study (Warmund and George 1990). Also, the early study, which included primarily thorny primocane-fruiting blackberry cultivars, demonstrated that the T_{50} values of 'Darrow' primary buds in January and late February were > 14 and 18 °C, respectively, lower than that of 'Navaho' buds. Additionally, the T_{50} values of 'Choctaw' primary buds in Jan and late Feb 1988 were 0.4 and 2.3 °C, respectively, lower than 'Navaho', indicating that genetic resources are available for enhanced cold hardiness in blackberry.

'Natchez' primary buds had the poorest survival among cultivars at all test dates. These results are similar to observations of McWhirt and Clark (2021) in which 'Natchez' suffered an estimated 20 to 40% primary bud injury, whereas 'Ouachita' and 'Ponca' buds had little apparent mortality after temperatures dropped as low as -28 to -18 °C across Arkansas in Feb 2021. In contrast to our study, primary buds of 'Ponca' also had little bud mortality in Arkansas, whereas they always had poorer survival than 'Ouachita' at all sampling dates in Missouri.

Table 3. Mean T_{50} values of primary flower buds of nine blackberry cultivars sampled from New Franklin, MO on 18 Nov 2023.

Cultivar	T_{50} value (°C)
Ouachita	-19.1 a [i]
Von	-17.7 b
Arapaho	-16.7 cd
Osage	-15.9 e
Apache	-17.3 bc
Navaho	-17.1 bc
Ponca	-15.7 e
Caddo	-16.1 de
Natchez	-12.7 f

[i] Means represent 5 replications of each 3-node cutting for each cultivar. LS-means followed by common letters do not differ at the 5% level of significance by Fisher's protected LSD test.

All cultivars in this study produced some reproductive secondary buds. However, secondary buds were sparse on all cultivars, except for 'Natchez'. At each sampling date, secondary buds of 'Natchez' survived lower temperatures than primary buds. In Jan, Feb, and Nov 2022, T_{50} values of 'Natchez' secondary buds were 7.2, 10.8, and 3.7 °C lower than its primary buds, respectively. These results confirm those reported in earlier studies where primary buds of other blackberry cultivars were generally injured at warmer temperatures than their secondary buds (Warmund and George, 1990). McWhirt and Clark (2021) also observed relatively high numbers of secondary buds on 'Natchez' and low numbers on 'Ouachita' and 'Osage'.

Although our study demonstrated that blackberry cultivars vary in their low-temperature survival, other researchers have suggested other factors that contribute to fruit production following exposure to freezing events. Following the unusual Feb 2021 freeze event described above and a -3 °C frost on 21 Apr 2021 in Arkansas, McWhirt and Clark (2021) reported that 'Ponca', 'Caddo', and 'Ouachita' had only an estimated 10% crop reduction. The relatively low crop loss from these cultivars was attributed to the fruit produced from high numbers of flower buds on basal canes originating from the crown of plants. In contrast, 'Osage' and 'Natchez' had ≥ 85% fruit yield reduction, which was attributed to their early bloom stage during the frost and the low numbers of reproductive buds near the base of the plants. In this report (McWhirt and Clark 2021), it was noted that 'Navaho' also tends to produce a significant number of inflorescences on basal canes. Thus, a high number of reproductive buds near the soil may influence overall flower bud survival on a whole-plant basis since temperatures may be slightly warmer near the soil surface than in the upper regions of the plant.

In a previous study with eastern thornless blackberry cultivars, relationships between leaf retention in autumn, primary reproductive buds, cane injury, and fruit yield were studied in Maryland (Kraut et al. 1986). Although early, hand-defoliation treatments in late September resulted in increased cane injury, these treatments did not affect mid-winter bud hardiness. The number of leaves retained in November and subsequent yield were negatively correlated. Although not specifically studied in our study, 'Natchez' was the only cultivar that had naturally defoliated by the November sampling dates in 2202 and 2023. When blackberry canes were collected in January, 'Ponca' and 'Caddo' were the only two cultivars that retained their leaves. Based on the high T_{50} values of 'Natchez' compared with other cultivars evaluated in this study in November and January, a relationship between primary bud hardiness and leaf retention was not apparent.

Conclusions

Although the temperature at which blackberry flower buds are injured during dormancy varies due to annual ambient weather conditions, the relative cold hardiness among cultivars evaluated in this study generally remained similar. At all test dates, 'Ouachita' primary flower buds had consistently low T_{50} values and high survival following low-temperature exposure. In contrast, 'Natchez' primary flower buds were injured at warmer temperatures than most other cultivars. However, 'Natchez' secondary buds were more cold-tolerant than its primary buds. Despite the superior cold hardiness of 'Ouachita' primary buds in this study, increased avoidance of blackberry flower bud freezing via genetic improvement is still needed for cold climates without the additional cost of rowcovers or structures for winter protection.

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