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Floral Morphology Differs Among New Northern Highbush Blueberry Cultivars

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Abstract

Variation in floral morphology and timing of bloom are common among cultivars of northern highbush blueberry (*Vaccinium corymbosum* L.). These differences can affect the ability of commercial pollinators to effectively pollinate and fertilize ovules, which can impact fruit set, berry size, and ultimate yields. New northern highbush blueberry cultivars may exhibit differences in flower morphology, which could impact pollination and fruit set. Evaluation of new cultivars compared to standard industry cultivars is of specific importance in predicting potential pollination constraints by honey bee (*Apis mellifera*), one of the primary pollinators in North America, and in developing optimal hive stocking densities. Three new cultivars ('Blue Ribbon', 'Top Shelf', and 'Cargo') were compared to an industry standard ('Duke') for floral morphology and relative bloom phenology. All new cultivars had significantly smaller flowers as compared to 'Duke'; however, 'Top Shelf' flowers exhibited a unique characteristic whereby many flowers (81%) had partially fused petals. Reduced flower size of new cultivars suggests floral morphology may be a constraint to effective pollination by honey bees and/or these cultivars will require higher honey bee stocking densities for effective pollination. However, the partially unfused petals in 'Top Shelf' may provide improved exposure to the stamen and pistil, which could increase accessibility to pollinators like honey bee and promote pollination and fruit set.

Keywords: *Vaccinium corymbosum;* Bloom; Pollination; Fruit set

Introduction

Increased consumption of blueberries (*Vaccinium* sp.) resulting in part from marketing campaigns which have advertised the health benefits of eating blueberries, has led to increased global and United States (US) production [1]. Northern highbush blueberry (*Vaccinium corymbosum*) is particularly important as an agricultural crop in the Pacific Northwest (PNW). Washington State, which leads US production of cultivated blueberry, produced 54,000 metric tons of blueberries from 5,423 ha in 2016; the value of utilized production was approximately $94 million US dollars [2]. With a growing global market, new cultivars are continually being developed by plant breeding programs and evaluated for environmental adaptation, tolerance/resistance to pest and disease pressures, and consumer preference [3].

Pollination and subsequent fruit set is a primary horticultural constraint for blueberry growers in the PNW [4,5]. In the PNW, honey bees (*Apis mellifera*) are the principal commercial pollinator for blueberry, but pollination can be limited by inclement weather, especially when conditions are not suitable for foraging (e.g., air temperature below 13°C, wind speed above 19 km/hour, and precipitation) [6]. These conditions can be common during the blueberry bloom period in Washington and the PNW [7] and weather is likely the main limiting factor influencing honey bee activity and fruit set [8]. The timing and length of the bloom window can vary among cultivar and environmental conditions but is reported to last 5-12 days [9]. These differences may have an impact on pollination efficiency if the bloom window coincides with cool and/or wet spring conditions that are less favorable for honey bee foraging. A short bloom window that coincides with inclement weather conditions may also leave little time for honey bee pollination to occur.

Highbush blueberry flowers generally have a high degree of variability between cultivars but very little within [9]. Blueberry flowers are characterized by a bell-shaped corolla, with stamen and anthers inside and a stigma sometimes protruding through the opening of the corolla (Figure 1) [10]. Flowers also have elongated corolla tubes and poricidal anthers, which can decrease pollen accessibility to some insect pollinators [11].

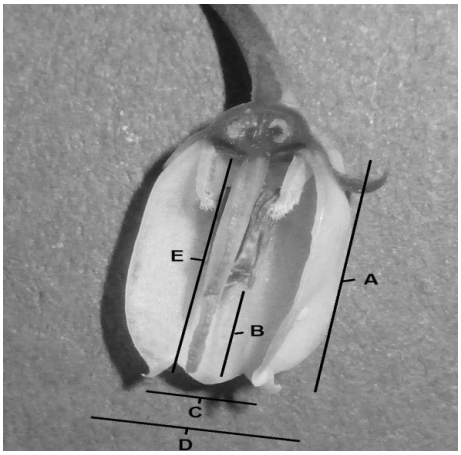

Figure 1: Cross-section of highbush blueberry (*Vaccinium corymbosum*) flower. A) Corolla length B) Distance between the anther and stigma C) Corolla aperture D) Corolla width and E) Style length.

Differences in the physical dimensions of flowers and their floral parts between cultivars can impact honey bee foraging and, as a result, fruit set [12]. The length and width of the corolla and diameter of the flower opening are likely among the more important floral traits impacting pollination and fertilization by honey bees in blueberry. Courcelles et al. [12] showed a clear relationship between floral

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morphology and honey bee visitation rates in widely planted cultivars ('Duke', 'Bluecrop', 'Draper' and 'Liberty') in British Columbia, Canada. 'Duke' is characterized by flowers with a large corolla aperture (throat diameter) and a flexible corolla, which allows honey bees to insert their heads into flowers and access pollen, despite their relatively short tongue length [3]. In support of this, Courcelles et al. [12] found flowers from 'Duke' plants were visited at a higher rate by honey bees compared to 'Draper' and 'Bluecrop'). Relative to 'Duke', the shorter corolla lengths of 'Bluecrop', 'Liberty', and 'Draper', combined with a smaller corolla aperture, reduced flower entry by the heads of honey bees. This in turn reduced the ability of honey bees to reach pollen, thereby reducing pollination.

Excluding 'Duke', cultivars selected for this trial are new and emerging with sizable plantings (Fall Creek Farm and Nursery, Inc., personal communication) [5]. 'Duke' is a widely planted cultivar with early fruit production and uniform fruit quality. It is a vigorous and hardy plant with an upright habit [13]. All three new cultivars selected ('Blue Ribbon', 'Top Shelf' and 'Cargo') were developed by Fall Creek (Fall Creek Farm and Nursery, Lowell, OR). 'Blue Ribbon' is a patented cultivar from Fall Creek that resulted from a cross with 'Toro' (female parent) and 'G344' (pollen parent). 'Blue Ribbon' is intended for the hand-harvest market and is a large berry reported to have exceptional flavor and a distinctive "crunch". It is an early-to-mid ripening cultivar that bears fruit approximately 1-2 weeks after 'Duke'. The plant is vigorous with a semi-upright/spreading habit [14]. 'Top Shelf' is also a patented cultivar from Fall Creek that resulted from crossing 'Magnolia' (female parent) and 'Draper' (pollen parent). It is a mid-season, exceptionally large berry reported to have excellent flavor. It is reported as consistently ripening approximately 2-3 weeks after 'Duke' and holds up well in storage. The plant is upright and vigorous with a vase shaped habit [15]. 'Cargo' was patented in 2013 by Fall Creek with 'Bluegold' and 'Ozarkblue' and the female and pollen parent, respectively. It flowers early, approximately the same time to a week after 'Duke'. This cultivar was developed for machine harvest and has uniform, medium-sized fruit that have good storage life and are reported to have excellent firmness. It is a vigorous plant with a narrow crown and upright habit [16].

Due to the impact of floral morphology and relative bloom phenology on pollination efficiency and subsequent fruit set, information on these characteristics will provide important indicators of potential pollination constraints and can also be utilized to estimate optimal hive density recommendations for promoting honey bee pollination and fruit set. The objective of this study was to assess and quantify the differences in bloom phenology and floral morphology between 'Duke', a standard cultivar in the PNW, and the new cultivars 'Blue Ribbon', 'Top Shelf' and 'Cargo'.

Materials and Methods

This experiment was conducted in 2016 and 2017 in a greenhouse at the Washington State University Northwestern Washington Research and Extension Center in Mount Vernon, WA (lat. 48°26' N, long. 122°23' W). The greenhouse was maintained between 13°C and 30°C from 1 Feb. to 30 June of both years. Temperature was recorded with a HOBO 4-channel external data logger (Onset Computer Corporation, Bourne, MA). The greenhouse was equipped with a thermostat outlet linked to a fan, which was set to ventilate the greenhouse at approximately 26°C. Relative humidity in the greenhouse was approximately 70%. We did not measure or manipulate light conditions, photoperiod during February was 10/14 (light/dark), and in March was 11/13. Four cultivars of highbush blueberry were grown in 3 L nursery stock containers provided by Fall Creek Farm and Nursery (Fall Creek, Oregon); plants were replaced each year. Cultivars consisted of 'Duke', 'Blue Ribbon', 'Top Shelf', and 'Cargo'. The plants were arranged in a randomized complete block design with four replications of 3 plants per treatment replicate (12 plants per replicate × 4 replications=48 plants total per year). Potted plants were arranged on a metal bench and grew in a proprietary substrate blend of Douglas Fir (*Pseudotsuga menziesii* L.) bark, perlite, and a controlled release fertilizer. Plants were watered 1 L per minute for 2 minutes twice daily with a model 1ZEHTMR hose timer (Rain Bird Corporation, Tucson AZ) and model 50950 stationary sprinkler (Fiskars Bands Inc., Middleton, WI).

Developmental stages were observed and recorded from the time plants were placed in the greenhouse through fruit ripening. Observed developmental stages included: 'early pink bud', 'early bloom' and 'full bloom'. Percent blue or ripe fruit was also observed. At full bloom, 10 flowers per plant were removed and dissected. Measurements of corolla length, corolla width (at the widest point of the flower), corolla aperture, anther to stigma distance and style length, as well as protrusion of the stigma through the corolla aperture were collected (Figure 1). Bumble bee (*Bombus vosnesenskii*) pollinators were placed in the greenhouse at approximately 20% full bloom. However, we are unable to present a statistical comparison of fruit set due to the young age of the plant material and the limited number of flowers after destructive sampling.

Data were analyzed for a randomized block design. The effects of year and block were analyzed with the *Ime4*, *Cor* and *Var* functions. Analysis of Variance (ANOVA) was done and mean separations were performed with Turkey's honestly significant difference (HSD) test (α=0.05; AGRICOLE package in R-studio). In the absence of year and block effects, years were combined and plants were analyzed by cultivar. All statistical analysis was carried out in R-studio statistical platform, using the 'cran', 'agricolae' and 'ggplot' statistical packages [16-18].

Results

Bloom timing and floral morphology differed between 'Duke', 'Blue Ribbon', 'Top Shelf' and 'Cargo' blueberry cultivars (*P*-value<0.001). Flowers of 'Duke' reached full bloom on 7 April 2016 and 10 April 2017, which was 4-8 days prior to any other cultivars included in the study. 'Blue Ribbon' reached full bloom approximately 5-7 days after 'Duke' (12 and 17 April 2016 and 2017, respectively). Both 'Top Shelf' and 'Cargo' reached full bloom on 16 and 22 April 2016 and 2017, respectively. Among the flowers left on plants that developed into fruit, 'Duke' berries ripened first, reaching 25%-75% blue on approximately 20 June 2016 and 25 June 2017. 'Blue Ribbon' followed 'Duke' reaching 25%-75% blue approximately 5-7 days later. 'Top Shelf' and 'Cargo' ripened approximately 15-17 days after 'Duke' in both years.

Flowers were different in size and morphological characteristics (Table 1). 'Duke' flowers were larger than all three of the new cultivars evaluated in this study. 'Blue Ribbon' flowers had the shortest and narrowest corollas with the smallest corolla aperture. 'Cargo' and 'Top Shelf' flowers were smaller than 'Duke' but were not significantly different from each-other in all but one measured morphological category (corolla aperture). The corolla aperture of 'Top Shelf' was significantly larger than both 'Blue Ribbon' and 'Cargo' and statistically similar in size to 'Duke' (Table 1). 'Top Shelf' also displayed unfused corollas in 81% of the flowers assessed (Figure 2).

	Corolla length (mm)	Corolla aperture (mm)	Corolla width (mm)	Distance between anther and stigma (mm)	Style length (mm)
Duke[z]	9.2 a[y]	4.8 a	8.9 a	2.8 a	6.0 a
Blue Ribbon	7.8 c	4.0 b	7.0 c	2.3 c	4.9 c
Top Shelf	8.1 bc	4.6 a	7.3 b	2.6 b	4.8 c
Cargo	8.4 b	3.9 b	7.3 b	2.5 b	5.7 b
P-value	<0.001	<0.001	<0.001	<0.001	<0.001

[z]Grown from 1-year nursery stock in 3 L pots under greenhouse conditions (n=12 plants/cultivar/year)
[y]Indicates mean separation at α=0.05 with Tukey's HSD

Table 1: Floral morphology of 'Duke', 'Blue Ribbon', 'Top Shelf' and 'Cargo' highbush blueberry (*Vaccinium corymbosum*). Values are means from 2016 and 2017.

Figure 2: Blueberry (*Vaccinium corymbosum*) flowers at 'full bloom' A) Duke B) Blue Ribbon C) Top Shelf and D) Cargo.

Discussion

Timing of bloom was consistent with the specifications from the nursery [13]. Namely, 'Duke' was the earliest to bloom ("very early"), followed by 'Blue Ribbon' ("Early/Mid"), 'Top Shelf' ("Mid"), and then 'Cargo' ("Late"). Generally concentrated bloom is desirable within a cultivar; however, a range in timing of development between cultivars is desirable for many growers in order to extend the harvest season and meet labor demands [12]. Timing of bloom is also important in blueberry because of the variation in spring weather conditions. Earlier blooming cultivars have a potentially higher chance of bloom coinciding with early spring weather systems that bring rain and cool temperatures, which are not optimal for honey bee pollination. Cultivars with a consistently later or longer bloom period may provide more opportunity for honey bees and other insect pollinators to forage assuming pollen viability is maintained, and stigmas are receptive to pollination [19]. The later bloom time of the three cultivars tested ('Top Shelf', 'Blue Ribbon' and 'Cargo') relative to 'Duke' suggests that weather conditions would potentially be less limiting for pollination due to the progression of the growing season and more mild weather conditions typical later in the spring season. Despite the more desirable flowering time (from a pollination perspective), the significantly smaller corolla aperture would still likely lead to pollination constraints among honey bees [12]. Subsequently, smaller flower size may necessitate higher honey bee stocking densities and/or the implementation of other strategies to promote pollination.

Floral morphological characteristics differed among cultivars. With the exception of a larger corolla aperture in 'Top Shelf', new cultivars had flowers smaller than 'Duke' in nearly all measured metrics. The larger flower opening in 'Top Shelf' may be attributed to the occurrence of partially fused petals in the corolla, which occurred in ~ 81% of flowers measured across both years (Figure 2C). Plants were re-ordered both years from the nursery making it unlikely that the unfused petals observed in 'Top Shelf' was a result of management in the greenhouse where the study was conducted or storage prior to placement in the greenhouse. The reason for the low number of blossoms remaining on the plants was because the nursery from which the plants were received from hedged the bushes, which removed many of the flower buds prior to shipping.

The accessibility of pollen and nectar rewards to honey bee is of importance for effective pollination [20]. Smaller corolla length, width, or corolla aperture, which was observed in the new cultivars, may negatively impact the accessibility of pollen to honey bees. Courcelles et al. [12] observed reduced visitation of honey bees (by ~ 50%) to flowers in the cultivars 'Draper', 'Bluecrop', and to some extent 'Liberty', as compared to 'Duke', all of which have smaller corolla lengths and apertures relative to 'Duke'. The only morphological metric in which 'Duke' was statistically different from the other three cultivars in that project was corolla aperture. Courcelles et al. [12] suggested corolla aperture and corolla width/flexibility likely influenced accessibility of floral parts to honey bees and overall honey bee flower preference. In this study, honey bee visitation and fruit set were not observed, however, significantly smaller flower size (corolla width) and corolla aperture were observed. Due to the importance of floral morphology on honey bee preference and pollination, 'Blue Ribbon' and 'Cargo' may be less preferred by honey bees and more difficult to pollinate because of reduced corolla width and aperture. While 'Top Shelf' flowers were smaller than 'Duke' in nearly all metrics evaluated, the corolla aperture size was approximately the same due to the common occurrence of unfused petals in the corolla (Figure 2C). The resultant space in unfused corollas of 'Top Shelf' would likely increase the flexibility of the corolla, thereby increasing honey bee access to floral parts.

As noted above, the partially fused petals of 'Top Shelf' may provide an improvement in availability of floral rewards to honey bees and other pollinators. In turn, this likely will increase the effectiveness of pollination, which could lead to greater fruit set and resultant yields in regions constrained by pollination. Additionally, it is possible that the partially unfused corolla could lead to increased occurrence of nectar robbing. This behavior was observed in the work by Courcelles et al. [12], whereby pollen bearing anthers were bypassed by some bees retrieving nectar from the base of the flower by damaging the corolla. The distance between the anther and stigma was also significantly less in all three new cultivars compared to 'Duke', something which was expected given the shorter overall length of the flower. The stigma of 'Duke' and 'Blue Ribbon' protruded 0.2-0.4 mm past the aperture of the corolla. It is unclear whether stigma protrusion impacts fertilization,

but many honey bees briefly land on flowers without successfully pollinating them [8,12,21,22]. Flowers with a protruding stigma may have increased chances of being exposed to pollen grains adhering to honey bees as compared to those with a stigma within the corolla, but data to support this are currently not available.

Conclusion

Of the three new cultivars evaluated in this experiment all had significantly smaller flowers than the industry standard 'Duke'. The small flower size may result in limited accessibility to pollen-bearing anthers and stigmas by honey bees and other pollinators. In turn, this may reduce pollination and subsequent fruit set, berry size, and crop yields, especially during seasons with reduced foraging due to inclement weather that is unconducive for pollinator activity, especially honey bees. The exception to this may be the partially unfused petals observed in most of the corollas of 'Top Shelf', which resulted in a larger and more flexible flower opening and potentially greater access to pollen and nectar resources. These results suggest that increased honey bee hive stocking densities or other pollination strategies may be necessary for effective pollination among these newly introduced cultivars. Additional research that evaluates the effects of these morphological differences on honey bee visitation and fruit set is recommended.

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