Nectar Production and Spectrum of Insect Visitors in Six Varieties of Highbush Blueberry (*Vaccinium corymbosum* L.) in SE Poland

Małgorzata Bożek

Department of Botany and Plant Physiology, University of Life Sciences in Lublin, Akademicka, 15, 20-950 Lublin, Poland

* To whom correspondence should be addressed. Email: malgorzata.bozek@up.lublin.pl

Abstract

The attractiveness of plants to pollinators depends strongly on flower rewards, especially nectar and pollen. Nectar mass, sugar concentration, and sugar mass are known to influence the spectrum and abundance of insect visitors. Respective data on nectar secretion in highbush blueberry (*Vaccinium corymbosum*) under the climatic conditions of Poland are scarce. This study was conducted in 2002–2005 to assess flower abundance, nectar production, and insect visitors in six varieties of *V. corymbosum* in Niemce, SE Poland. Flower abundance ranged from 1.63 ± 0.64 (‘Darrow’) to 4.07 ± 0.95 in thousands of flowers per shrub (‘Northland’). Nectar mass, sugar concentration, and nectar sugar mass increased with flower age, peaking between the sixth and ninth day. Significant differences in nectar characteristics occurred between years and between varieties. ‘Bluecrop’ and ‘Darrow’ produced the largest nectar mass (19.08 ± 7.09 and 16.60 ± 8.31 mg nectar per flower, respectively) and nectar sugar mass per flower (6.39 ± 1.52 and 5.76 ± 1.51 mg sugar per flower, respectively). The estimated sugar yield in the studied *V. corymbosum* varieties ranged from 9.4 ± 3.3 to 20.7 ± 3.8 g sugar per shrub (‘Croatan’ and ‘Bluecrop’, respectively). Regarding insect visitors, only honey bees and bumble bees were observed. Honey bees comprised 81%–98% of the total number of observed insect visitors. Highbush blueberry, due to abundant blooming and high per-flower sugar yield, is thus a good source of nectar sugars for honey bees.

Keywords

highbush blueberry; nectar production; nectar sugars; insect visitors; honey bees

1. Introduction

It has been estimated that over 75% of the globally most important food crops depend, to some extent, on animal pollination (Klein et al., 2007), and insect pollination was shown to enhance fruit and seed quantity and quality (Bisui et al., 2020; Bommarco et al., 2012; Castle et al., 2019; Garratt et al., 2014; Pereira et al., 2015; Sushil et al., 2013). However, over the past decades, severe losses in insect pollinator numbers and diversity have been reported (Cameron et al., 2011; Kevan & Phillips, 2001; Rhodes, 2018; Antoń & Denisow, 2018). The main causes of this phenomenon include agricultural intensification, spreading of insect pathogens, habitat loss, and shortage of food resources (Dance et al., 2017; Fürst et al., 2014; Jachula, Denisow, & Wrzesień, 2018; Loí et al., 2020; Wrzesiñ et al., 2016; Xiao et al., 2016), and it can reduce agricultural profitability (Gallai et al., 2009; Winfree et al., 2011) and threatens overall biodiversity (Brodie et al., 2014; Potts et al., 2010). Nectar is a floral reward that mediates mutualistic relationships between the majority of angiosperms and visiting insects (Bożek, 2019; Nepi et al., 2018; Palmer-Young...
Bożek / Nectar Production in Highbush Blueberry

et al., 2019); it is an aqueous solution of sugars and other minor constituents, e.g., amino acids, proteins, alkaloids, phenolics, and metal ions (Nicolson & Thornburg, 2007; Roy et al., 2017) and is considered an important source of energy to pollinators (Hayashi et al., 2016; Somme et al., 2015). Nectar secretion patterns, sugar concentration, nectar sugar mass, and nectar chemical composition (primarily sugar and amino acid composition) are crucial factors affecting insect visitor guilds as well as frequency and duration of visits to flowers (Brown & Brown, 2020; Jachula et al., 2019; Nepi et al., 2018; Shackleton et al., 2016; Strzałkowska-Abramek, 2019).

The reproductive success of entomophilous plant species depends on insect activity which is influenced by nectar availability (Denisow et al., 2016, 2018; Heil, 2011; Liu et al., 2015; Zhao et al., 2014). Studies on nectar production may thus be useful to estimate a plant’s attractiveness to pollinators (Masierowska & Piętka, 2014; Nagy-Déri et al., 2013; Schmidt et al., 2015), which in turn affects yield and quality of fruit and seeds (Bożek, 2012; Quinet et al., 2016), even in self-fertile taxa (de O. Millont et al., 2013; Denisow, 2002).

Highbush blueberry (Vaccinium corymbosum) has become a popular commercial crop in Europe. This species has attracted attention due to its pleasantly sweet fruits which are also a source of biologically active compounds, especially antioxidants (Cardeñoza et al., 2016; Pervin et al., 2016). Poland is one of the leading producers of blueberries – in 2019, total fruit yield exceeded 25,000 tons, and approximately 6,700 tons of fruit were exported, predominantly to countries of the European Union (Statistics Poland, 2019). However, data on nectar production by highbush blueberry under the climatic conditions of Poland are scarce and were collected only regarding very young shrubs (Jabłoński et al., 1983).

The present study was conducted to examine nectar production and insect visitors in six varieties of V. corymbosum. In particular, (i) diurnal patterns of flowering and flower abundance, (ii) nectar secretion dynamics and nectar sugar yield, and (iii) the spectrum of insect visitors were investigated.

2. Material and Methods

2.1. Varieties and Study Site

The study was carried out from 2002 to 2005. Six V. corymbosum varieties were used, i.e., 'Bluecrop,' 'Bluejay,' 'Croatan,' 'Darrow,' 'Northland,' and 'Spartan,’ which had been grown in Niemce (51°22’ N, 22°38’ E; south-eastern Poland) on a farm covering 0.25 ha, established in 1993. The shrubs had been planted at 2 m × 1 m spacing (5,000 plants/ha). In the local climate, V. corymbosum blooms in May or June (Bożek, 2009).

2.2. Blooming and Insect Visitors

To assess flower abundance per shrub, each variety’s number of flowers per inflorescence (n = 15), number of inflorescences per shoot (n = 15), and number of shoots per shrub (n = 15) were counted and multiplied, respectively. The spectrum and abundance of insect visitors/m² were recorded during full flowering. Observations were carried out for 5 min in 1-hr intervals between 6 a.m. and 8 p.m. (GMT + 2 hr) for 3 consecutive days.

2.3. Nectar Production

Nectar production was evaluated during full flowering. The pipette method described by Jabłoński (2002) was used. To prevent nectar collection by insect visitors before sampling, inflorescences were covered using tulle bags. The dynamics of nectar production were monitored at different stages of flower development (interval = 1 day) from the budding stage (1–2 hr before flower opening; ‘Day 0’) until corolla wilting. Nectar was collected using tarred glass pipettes, with 12 replications. A single sample contained nectar of 5–10 flowers. The concentration of sugars (% w/w) in nectar was measured using an Abbe refractometer (Carl Zeiss AG,
Jena, Germany). Using nectar mass and nectar sugar concentration data, nectar sugar mass (at the peak of nectar sugar secretion) was calculated per flower and per shrub.

2.4. Weather Conditions

Meteorological data were collected from a weather station in Niemce. Mean air temperature and precipitation data of 2002–2005 were compared to long-term data collected in 1951–2005 (Table 1). Regarding the month of April, the highest air temperatures were recorded in 2002 and 2005, which exceeded the long-term norm by 1.1 and 1.6 °C, respectively; in these periods, 50% less precipitation than usual was recorded. The highest air temperatures of the month of May were recorded in 2002 and 2003. In May 2005, heavy rainfalls occurred, and precipitation exceeded the long-term norm by more than 60%.

2.5. Data Analyses

Data were analyzed using STATISTICA software v.13.1 (StatSoft Poland, Cracow, Poland). Before analyses, data distribution was tested for normality. Data on nectar mass per flower and sugar mass per flower were log\(_{10}\)-transformed; data on numbers of flowers per shrub and on sugar mass per shrub were square-root transformed.

A one-way analysis of variance was applied to test differences between years and between varieties. Means were compared post hoc using Tukey’s HSD test at \(\alpha = 0.05\).

3. Results

The diurnal pattern of blooming was similar between varieties; therefore, only that of ‘Bluecrop’ is described. Bloom development peaked in the evening hours (Figure 1). The number of flower buds that opened between 6 p.m. and 7 p.m. constituted approximately 30% of the total number of flowers developed throughout the day. Both number of flowers per inflorescence and number of inflorescences per shrub differed between years (\(F_{3, 356} = 16.011; p < 0.001\) and \(F_{3, 356} = 11.661; p = 0.001\), respectively) and varieties (\(F_{5, 354} = 5.046; p < 0.001\) and \(F_{5, 354} = 45.481; p < 0.001\), respectively) (Table 2). Consequently, effects of year (\(F_{3, 354} = 3.457; p = 0.019\)) and variety (\(F_{5, 354} = 35.549; p < 0.001\)) on the number of flowers per shrub were observed. Flowering was most abundant in variety ‘Northland’ and least abundant in ‘Darrow’ (4.07 ± 0.95 vs. 1.63 ± 0.64, in thousands of flowers per shrub, respectively).

As demonstrated for ‘Bluecrop’ (Figure 2), nectar mass, sugar concentration, and nectar sugar mass increased throughout flower development and peaked between the sixth and ninth day of the flowers’ life-span. Similar patterns were also observed in the other varieties. The mass of produced nectar differed significantly between years (\(F_{3, 284} = 20.464; p < 0.001\); highest values recorded in 2005) and varieties (\(F_{5, 282} = 31.87; p = 0.002\); Table 3). The highest per-flower nectar production occurred in ‘Bluecrop’ and ‘Darrow’ (19.08 ± 7.09 mg and 16.60 ± 8.31 mg nectar per flower, respectively). Nectar sugar concentrations differed significantly between years (\(F_{3, 284} = 24.283; p = 0.004\) and varieties (\(F_{5, 282} = 4.351; p < 0.001\)). Nectar sugar mass was affected by year (\(F_{3, 284} = 6.781; p = 0.002\)) and variety (\(F_{5, 282} = 28.767; p < 0.001\)).
Figure 1  Diurnal pattern of flowering expressed as numbers of newly opened flowers in 1-hr intervals in relation to the total number of newly opened flowers throughout the day, and diurnal frequency of insect visitors of *Vaccinium corymbosum* 'Bluecrop' observed in Niemce, SE Poland. Shown are mean values over the years of the study.

Figure 2  Effect of flower age on nectar mass per flower, nectar sugar concentration, and nectar sugar mass per flower in *Vaccinium corymbosum* 'Bluecrop.' Shown are the means ± SD (vertical bars) calculated across the years of the study.

'Bluecrop' and 'Darrow' produced the largest sugar mass per flower (6.39 ± 1.52 mg and 5.76 ± 1.51 mg sugar per flower, respectively). Sugar yield per shrub differed significantly between years ($F_{3, 354} = 5.546; p = 0.001$) and varieties ($F_{5, 354} = 22.913; p < 0.001$), and the estimated sugar yield ranged between 9.4 ± 3.3 g and 20.7 ± 3.8 g sugar per shrub, with the highest yield recorded in 'Bluecrop' (Figure 3).

Regarding insect visitors, only honey bees and bumble bees were observed (Figure 4). Depending on the variety, honey bee workers comprised 81%–98% of the total number of insect visitors. Visits of honey bees were distributed evenly throughout the day, while foraging activity of bumble bees peaked in the morning (9 a.m.–10 a.m.) and afternoon hours (6 p.m.–7 p.m.; Figure 1).

4. Discussion

Nectar mass, sugar concentration, and sugar mass in flowers of *V. corymbosum* varied between years of the present study. Variability between years was particularly prominent in 'Darrow.' In this variety, the largest difference in nectar mass was approximately threefold (8.41 ± 2.38 mg nectar per flower in 2002 and 25.78 ± 9.53 mg nectar per flower in 2005), and the difference in sugar concentration was approximately twofold between years (53.7% ± 10.5% in 2002 and 26.8% ± 9.8%...
### Table 2 Flower abundance in six *Vaccinium corymbosum* varieties in 2002–2005 in Niemce, SE Poland.

| Variety   | Year | No. of flowers/1 inflorescence (mean ± SD) | No. of inflorescences/1 shrub (thous.) (mean ± SD) | No. of flowers/1 shrub (thous.) (mean ± SD) |
|-----------|------|------------------------------------------|---------------------------------|---------------------------------|
| 'Bluecrop' | 2002 | 7.8 ± 3.0a                               | 0.42 ± 0.04ab                   | 3.28 ± 0.31a                    |
|           | 2003 | 7.5 ± 2.1a                               | 0.37 ± 0.05a                    | 2.80 ± 0.41a                    |
|           | 2004 | 7.5 ± 1.6a                               | 0.51 ± 0.18b                    | 3.82 ± 1.38b                    |
|           | 2005 | 7.1 ± 1.5a                               | 0.42 ± 0.07ab                   | 3.01 ± 0.47a                    |
| Mean      |      | 7.5 ± 2.1B                               | 0.43 ± 0.11C                    | 3.23 ± 0.86C                    |
| 'Bluejay'  | 2002 | 7.8 ± 1.8b                               | 0.38 ± 0.04a                    | 2.95 ± 0.28a                    |
|           | 2003 | 6.9 ± 1.9ab                               | 0.38 ± 0.09a                    | 2.61 ± 0.59a                    |
|           | 2004 | 5.8 ± 1.6a                               | 0.40 ± 0.04a                    | 2.34 ± 0.21a                    |
|           | 2005 | 6.6 ± 1.6a                               | 0.43 ± 0.07a                    | 2.84 ± 0.45a                    |
| Mean      |      | 6.8 ± 1.9AB                               | 0.40 ± 0.06BC                   | 2.69 ± 0.47BC                   |
| 'Croatan'  | 2002 | 7.3 ± 2.2b                               | 0.24 ± 0.04a                    | 1.77 ± 0.25a                    |
|           | 2003 | 6.1 ± 1.6a                               | 0.26 ± 0.04a                    | 1.60 ± 0.25a                    |
|           | 2004 | 6.1 ± 1.8a                               | 0.39 ± 0.03b                    | 2.38 ± 0.21b                    |
|           | 2005 | 6.2 ± 1.6a                               | 0.45 ± 0.06c                    | 2.82 ± 0.40b                    |
| Mean      |      | 6.4 ± 1.9A                               | 0.34 ± 0.10B                    | 2.14 ± 0.56B                    |
| 'Darrow'   | 2002 | 8.6 ± 2.2b                               | 0.16 ± 0.03a                    | 1.33 ± 0.23ab                   |
|           | 2003 | 6.2 ± 2.0a                               | 0.17 ± 0.02a                    | 1.04 ± 0.15a                    |
|           | 2004 | 6.4 ± 1.5a                               | 0.38 ± 0.10c                    | 2.42 ± 0.63c                    |
|           | 2005 | 6.6 ± 1.8a                               | 0.26 ± 0.04b                    | 1.70 ± 0.29bc                   |
| Mean      |      | 7.0 ± 2.1AB                               | 0.24 ± 0.11A                    | 1.63 ± 0.64A                    |
| 'Northland'| 2002 | 8.0 ± 1.6a                               | 0.49 ± 0.11a                    | 3.94 ± 0.92a                    |
|           | 2003 | 7.1 ± 2.1a                               | 0.52 ± 0.07a                    | 3.53 ± 0.50a                    |
|           | 2004 | 7.4 ± 1.7a                               | 0.67 ± 0.11b                    | 5.00 ± 0.81b                    |
|           | 2005 | 7.5 ± 1.7a                               | 0.51 ± 0.11a                    | 3.83 ± 0.80a                    |
| Mean      |      | 7.5 ± 1.9B                               | 0.54 ± 0.13D                    | 4.07 ± 0.95D                    |
| 'Spartan'  | 2002 | 7.8 ± 1.6b                               | 0.41 ± 0.03a                    | 3.21 ± 0.20a                    |
|           | 2003 | 6.4 ± 2.2a                               | 0.46 ± 0.04ab                   | 2.87 ± 0.26a                    |
|           | 2004 | 7.1 ± 1.4ab                               | 0.48 ± 0.07b                    | 3.39 ± 0.52b                    |
|           | 2005 | 6.8 ± 2.2ab                               | 0.45 ± 0.05ab                   | 3.06 ± 0.31a                    |
| Mean      |      | 7.0 ± 2.0AB                               | 0.45 ± 0.05C                    | 3.13 ± 0.40C                    |

Means ± standard deviation (SD); same lower-case letters indicate no significant difference between years; same capital letters indicate no significant difference between varieties (*α* = 0.05; Tukey's HSD test).

...in 2005). Irrespective of the variety, the highest nectar mass was recorded in 2005, when precipitation exceeded the long-term norm by 60%. Nectar production depends strongly on a range of abiotic factors such as precipitation, air temperature, air humidity, light availability, and CO₂ concentration, and significant interannual variation in nectar and sugar quantity were reported by numerous studies (Denisow et al., 2014; Enkegaard et al., 2016; Jachula et al., 2019; Jachula, Konarska, & Denisow, 2018). Nectar characteristics also differed between varieties, e.g., nectar mass per flower was more than twofold higher in 'Bluecrop' than in 'Darrow.' Differences in nectar production between varieties is a known phenomenon which suggests the importance of genetic factors regarding nectar secretion (Bertazzini & Forlani, 2016; Bożek & Wieniarska, 2006; Masierowska & Piętka, 2014).

The studied *V. corymbosum* varieties produced considerable numbers of flowers, which, together with high per-flower sugar mass, resulted in high sugar yield per shrub, ranging from 9.4 to 20.7 g ('Bluecrop' and 'Darrow,' respectively). Thus, approximately 47.0–103.5 kg nectar sugars can be expected from 1 ha highbush blueberry crop. In the current study, the estimated sugar productivity of 'Bluecrop' and 'Darrow' was two- to threefold higher than that estimated by Jabłoński.
Table 3  Nectar mass, nectar sugar concentration, and nectar sugar mass (at the peak of nectar secretion) in six *Vaccinium corymbosum* varieties in 2002–2005, Niemce, SE Poland.

| Variety | Year | Mass of nectar/1 flower (mg) (mean ± SD) | Sugar concentration (%) (mean ± SD) | Mass of nectar sugars/1 flower (mg) (mean ± SD) |
|---------|------|----------------------------------------|------------------------------------|--------------------------------------------|
| 'Bluecrop' | 2002 | 10.42 ± 2.62a | 53.5 ± 7.7b | 5.47 ± 1.12a |
|         | 2003 | 19.66 ± 3.96b | 30.6 ± 9.6a | 5.71 ± 0.97a |
|         | 2004 | 19.45 ± 1.93b | 33.8 ± 4.2a | 6.62 ± 1.25ab |
|         | 2005 | 26.77 ± 6.34c | 29.7 ± 5.3a | 7.78 ± 1.51b |
| Mean    |      | 19.08 ± 7.09B | 36.9 ± 12.0A | 6.39 ± 1.52B |
| 'Bluejay' | 2002 | 8.78 ± 1.07a | 47.6 ± 9.2b | 4.19 ± 1.03ab |
|         | 2003 | 7.91 ± 1.95a | 39.8 ± 8.6a | 3.15 ± 0.99a |
|         | 2004 | 6.92 ± 1.07a | 50.1 ± 8.7b | 3.42 ± 0.62a |
|         | 2005 | 12.84 ± 3.99b | 41.7 ± 8.9a | 5.34 ± 2.03b |
| Mean    |      | 9.11 ± 3.25A | 44.8 ± 9.8B | 4.02 ± 1.54A |
| 'Croatan' | 2002 | 11.55 ± 2.39b | 36.3 ± 6.4a | 4.08 ± 0.65ab |
|         | 2003 | 11.04 ± 1.65b | 41.5 ± 5.5ab | 4.53 ± 0.59b |
|         | 2004 | 7.56 ± 1.34a | 44.8 ± 5.3b | 3.34 ± 0.39a |
|         | 2005 | 12.72 ± 2.29b | 43.3 ± 10.4ab | 5.37 ± 1.08c |
| Mean    |      | 10.72 ± 2.75A | 41.5 ± 7.9AB | 4.33 ± 1.03A |
| 'Darrow' | 2002 | 8.41 ± 2.38a | 53.7 ± 10.5b | 4.41 ± 1.4a |
|         | 2003 | 16.73 ± 4.34b | 34.3 ± 4.5a | 5.69 ± 1.48ab |
|         | 2004 | 15.47 ± 2.91b | 45.2 ± 8.7b | 6.80 ± 0.84b |
|         | 2005 | 25.78 ± 9.53c | 26.8 ± 9.8a | 6.14 ± 1.1b |
| Mean    |      | 16.60 ± 8.31B | 40.0 ± 13.4AB | 5.76 ± 1.51B |
| 'Northland' | 2002 | 10.96 ± 4.03b | 40.6 ± 14.6a | 3.92 ± 0.63b |
|         | 2003 | 7.91 ± 1.82a | 44.3 ± 7.5a | 3.39 ± 0.51ab |
|         | 2004 | 5.83 ± 1.2a | 51.8 ± 7.6b | 3.00 ± 0.65a |
|         | 2005 | 11.73 ± 2.71b | 41.6 ± 9.2a | 4.68 ± 0.73c |
| Mean    |      | 9.11 ± 3.57A | 44.6 ± 11.0B | 3.75 ± 0.89A |
| 'Spartan' | 2002 | 8.14 ± 1.67a | 53.6 ± 5.9b | 4.36 ± 0.98ab |
|         | 2003 | 11.58 ± 2.62b | 40.2 ± 10.1a | 4.54 ± 1.19b |
|         | 2004 | 6.41 ± 1.13a | 49.1 ± 7.4b | 3.17 ± 0.81a |
|         | 2005 | 12.25 ± 2.58b | 39.0 ± 12.6a | 4.66 ± 1.49b |
| Mean    |      | 9.59 ± 3.19A | 45.5 ± 11.2B | 4.18 ± 1.29A |

Means ± standard deviation (SD); same lower-case letters indicate no significant difference between years; same capital letters indicate no significant difference between varieties (α = 0.05; Tukey's HSD test).

Means ± standard deviation (SD); same lower-case letters indicate no significant difference between years; same capital letters indicate no significant difference between varieties (α = 0.05; Tukey's HSD test).

et al. (1983); however, this previous study assessed sugar mass in young (3–4 years old) shrubs, and the authors emphasized that a considerably higher yield can be expected in older shrubs. High sugar productivity by highbush blueberry places this species among the best sugar-yielding cultivated shrubs in the Polish climate. For comparison, the estimated sugar yield of black currant is 4–7 kg/ha (Jabłoński et al., 1997), and that of raspberry is 39–41 kg/ha (Szklanowska et al., 1989).

In flowers of *V. corymbosum*, anthers open through pores at the tips (Courcelles et al., 2013), thus pollen can be released through sonication by insects, suggesting the so-called buzz-pollination syndrome (Hoffman et al., 2018). This trait can strongly affect pollinator efficiency (Courcelles et al., 2013), and more than 50 Apoidea genera are known to collect pollen released from anthers by sonication (e.g., *Bombus* spp., *Xylocopa* spp., and *Andrena* spp.); however, this does not occur in *Apis mellifera* (de Luca & Vallejo-Marín, 2013). Nonbuzzing insects can collect only small amounts of pollen from buzz-pollinated flowers, thus they are considered low-efficiency pollinators (dos Santos et al., 2009; Solís-Montero et al., 2015). According to my observations, honey bees were interested only in nectar. It was shown, however,
Figure 3 Nectar sugar mass per shrub (mean ± SD) in six *Vaccinium corymbosum* varieties in 2002–2005. Same lower-case letters indicate no significant difference between years, and same capital letters indicate no significant difference between varieties (α = 0.05; Tukey’s HSD test).

Figure 4 Proportional contribution of insect guilds visiting six *Vaccinium corymbosum* varieties in Niemce, SE Poland. Data of 2002–2005 are shown.

that even when not collecting pollen from corbiculae, *A. mellifera* can assume substantial amounts of pollen on its body while foraging for nectar (up to 713 ± 128 pollen tetrads of *V. corymbosum*) and thereby contribute to pollination (Hoffman et al., 2018). This, in turn, may explain high the fruit set in highbush blueberry when flowers were visited mainly by honey bees (Bożek, 2009). Beside the specific anther structural characteristics, flowers of some *V. corymbosum* varieties show long, narrow corollas (e.g., ‘Bluecrop’) and seem to be adapted to pollination by insects with long mouthparts. According to Courcelles et al. (2013), over 40% of visits made by honey bees to ‘Bluecrop’ flowers were illegitimate, i.e., the bees sucked nectar by inserting their proboscis between the flower corolla and the inferior ovary (thereby avoiding touching the anthers); the authors also observed that *A. mellifera*, when foraging legitimately, inserted not only the proboscis but also pushed their head into the flower to reach nectar. I did not notice nectar robbing in any of the studied variety but frequently observed honey bees inserting their whole heads in the corolla.

In the USA, which is where highbush blueberry occurs naturally, the most frequent flower foragers were *Andrena* spp., *Bombus* spp., and *Xylocopa virginica* (MacKenzie & Eickwort, 1996; Scott et al., 2016). A previous study on nectar production and pollination in *V. corymbosum* in the Polish climate showed that flowers are visited mainly by honey bees and occasionally by bumble bees, *Andrena* spp., and *Megachile* spp. (Jabloński et al., 1983). In the present study, only honey bees (>80% of insect visitors) and bumble bees were observed to forage on *V. corymbosum* flowers. The low abundance of bumble bees and lack of other wild pollinators of highbush blueberry may result from competition with honey bees. Increasing evidence suggests that high abundances of honey bees can reduce population sizes of wild pollinators (Geldmann & González-Varo, 2018; Jachuła et al., 2020; Lindström et al., 2016; Thomson, 2016).
In conclusion, *V. corymbosum* is an important food crop in agricultural areas. This species flowers abundantly and produces large amounts of nectar sugars. Highbush blueberry can add to spring and late spring sugar resources, which is especially important for honey bees.

**References**

Antoń, S., & Denisow, B. (2018). Floral phenology and pollen production in the five nocturnal *Oenothera* species (Onagraceae). *Acta Agrobotanica, 71*(2), Article 1738. https://doi.org/10.5586/aa.1738

Bertazzini, M., & Foiani, G. (2016). Intraspecific variability of floral nectar volume and composition in rapeseed (*Brassica napus* var. *oleifera*). *Frontiers in Plant Science, 7*, Article 288. https://doi.org/10.3389/fpls.2016.00288

Bisui, S., Layek, U., & Karmakar, P. (2020). Utilization of Indian dammar bee (*Tetragonula iridipes Smith*) as a pollinator of bitter gourd. *Acta Agrobotanica, 73*(1), Article 7316. https://doi.org/10.5586/aa.7316

Bożek, M. (2012). The effect of pollinating insects on fruiting of two cultivars of *Lonicera caerulea* L. *Journal of Apicultural Science, 56*(2), 5–11. https://doi.org/10.2478/v10289-012-0018-6

Bożek, M. (2019). Nectar secretion and pollen production in *Hyacinthus orientalis* 'Sky Jacket' (Asparagaceae). *Acta Agrobotanica, 72*(4), Article 1796. https://doi.org/10.5586/aa.1796

Bożek, M., & Wieniarska, J. (2006). Biologia kwitnienia i wydajność cukrowa kwiatów dwóch odmian *Lonicera kamtschatica* (Sevast.) Pojark [Blooming biology and sugar efficiency of two cultivars of *Lonicera kamtschatica* (Sevast.) Pojark]. *Acta Agrobotanica, 59*(1), 177–182. https://doi.org/10.5586/aa.2006.018

Brodie, J. E., Aslan, C. E., Rogers, H. S., Redford, K. H., Maron, J. L., Bronstein, J. L., & Groves, C. R. (2014). Secondary extinctions of biodiversity. *Trends in Ecology and Evolution, 29*(12), 664–672. https://doi.org/10.1016/j.tree.2014.09.012

Brown, M., & Brown, M. J. F. (2020). Nectar preferences in male bumblebees. *Insectes Sociaux, 67*, 221–228. https://doi.org/10.1007/s00442-012-271-6

Castle, D., Grass, I., & Westphal, C. (2019). Fruit quantity and quality of strawberries benefit from enhanced pollinator abundance at hedgerows in agricultural landscapes. *Agriculture, Ecosystems and Environment, 275*, 14–22. https://doi.org/10.1016/j.agee.2019.01.003

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America, 108*(2), 662–667. https://doi.org/10.1073/pnas.1014743108

Cardenosa, V., Girones-Vilaplana, A., Muriel, J. L., Moreno, D. A., & Moreno-Rojas, J. M. (2016). Influence of genotype, cultivation system and irrigation regime on antioxidant capacity and selected phenolics of blueberries (*Vaccinium corymbosum* L.). *Food Chemistry, 202*, 276–283. https://doi.org/10.1016/j.foodchem.2016.01.118

Courcelles, D., Button, L., & Elle, E. (2013). Bee visit rates vary with floral morphology among highbush blueberry cultivars (*Vaccinium corymbosum* L.). *Journal of Applied Entomology, 137*(9), 693–701. https://doi.org/10.1111/jen.12059

Dance, C., Botías, C., & Goulson, D. (2017). The combined effects of a monotonous diet and exposure to thiamethoxam on the performance of bumblebee micro-colonies. *Ecotoxicology and Environmental Safety, 139*, 194–201. https://doi.org/10.1016/j.ecoenv.2017.01.041

de Luca, P. A., & Vallejo-Marín, M. (2013). What's the "buzz" about? The ecology and evolutionary significance of buzz-pollination. *Current Opinion in Plant Biology, 16*(4), 429–435. https://doi.org/10.1016/j.pbi.2013.05.002

de O. Milfont, M., Rocha, E. E. M., Lima, A. O. N., & Freitas, B. M. (2013). Higher soybean production using honeybee and wild pollinators, a sustainable alternative to pesticides and autopollination. *Environmental Chemistry Letters, 11*, 335–341. https://doi.org/10.1007/s10311-013-0412-8

Denisow, B. (2002). The influence of the degree of pollination of black currant flowers (*Rubus nigrum* L.) on the number of seeds in fruits and its size. *Annales Universitatis Mariae Curie-Skłodowska, Sectio EEE Horticultura, 11*, 11–18.
Denisow, B., Masierowska, M., & Antoń, S. (2016). Floral nectar production and carbohydrate composition and the structure of receptacular nectaries in the invasive plant Bunias orientalis L. (Brassicaceae). *Protoplasma*, 253(6), 1489–1501. https://doi.org/10.1007/s00709-015-0902-6

Denisow, B., Strzałkowska-Abramek, M., Bożek, M., & Jeżak, A. (2014). Early spring nectar and pollen and insect visitor behavior in two Corydalis species (Papaveraceae). *Journal of Apicultural Research*, 53(1), 93–102. https://doi.org/10.2478/jas-2014-0009

Denisow, B., Strzałkowska-Abramek, M., & Wrzesień, M. (2018). Nectar secretion and pollen production in protandrous flowers of *Campanula patula* L. (Campanulaceae). *Acta Agrobotanica*, 71(1), Article 1734. https://doi.org/10.5586/aa.1734
dos Santos, S. A. B., Roselino, A. C., Hrcnir, M., & Bego, L. R. (2009). Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). *Genetics and Molecular Research*, 8(2), 751–757. https://doi.org/10.4238/vol8-2kerr015

Enkegaard, A., Kryger, P., & Boelt, B. (2016). Determinants of nectar production in heather. *Journal of Apicultural Research*, 55(1), 100–106. https://doi.org/10.1080/00218839.2016.1192342

Fürst, M. A., McMahon, D. P., Osborne, J. L., Paxton, R. J., & Brown, M. J. F. (2014). Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature*, 506(7488), 364–366. https://doi.org/10.1038/nature12977

Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, 68(3), 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garratt, M. P. D., Breeze, T. D., Jenner, N., Police, C., Biesmeijer, J. C., & Potts, S. G. (2014). Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. *Agriculture, Ecosystems and Environment*, 184, 34–40. https://doi.org/10.1016/j.agee.2013.10.032

Geldmann, J., & González-Varo, J. P. (2018). Conserving honey bees does not help wildlife. *Science*, 359(6374), 392–393. https://doi.org/10.1126/science.aar2269

Hayashi, M., Nakamura, J., Sasaki, K., & Harano, K.-I. (2016). Honeybee males use highly concentrated nectar as fuel for mating flights. *Journal of Insect Physiology*, 93–94, 50–55. https://doi.org/10.1016/j.jinsphys.2016.08.007

Heil, M. (2011). Nectar: Generation, regulation and ecological functions. *Trends in Plant Science*, 16(4), 191–200. https://doi.org/10.1016/j.tplants.2011.01.003

Hoffman, G. D., Lande, C., & Rao, S. (2018). A novel pollen transfer mechanism by honey bee foragers on highbush blueberry (Ericales: Ericaceae). *Environmental Entomology*, 47(6), 1465–1470. https://doi.org/10.1093/earljee/nvy162

Jabłoński, B. (2002). Notes on the method to investigate nectar secretion rate in flowers. *Journal of Apicultural Research*, 46(2), 117–125.

Jabłoński, B., Kołtowski, Z., & Szklanowska, K. (1997). Nektarowanie i wydajność cukrowa ważniejszych odmian porzeczki czarnej (*Ribes nigrum* L.) [Nectar secretion and sugar efficiency of some cultivars of black currant (*Ribes nigrum* L.)]. *Pszczelnicze Zeszyty Naukowe*, 41, 7–17.

Jabłoński, B., Król, S., Pliszka, K., & Żurowski, Z. (1983). Nektarowanie i wydajność cukrowa *Vaccinium corymbosum* L. [Nectar production and pollination of highbush blueberry (*Vaccinium corymbosum* L.)]. *Pszczelnicze Zeszyty Naukowe*, 27, 91–109.

Jachuła, J., Denisow, B., & Wrzesień, M. (2018). Validation of floral food resources for pollinators in agricultural landscape in SE Poland. *Journal of the Science of Food and Agriculture*, 98(7), 2672–2680. https://doi.org/10.1002/jsfa.8761

Jachuła, J., Konarska, A., & Denisow, B. (2018). Micromorphological and histochemical attributes of flowers and floral reward in *Linaria vulgaris* (Plantaginaceae). *Protoplasma*, 255(6), 1763–1776. https://doi.org/10.1007/s00709-018-1269-2

Kevan, P. G., & Phillips, T. P. (2001). The economic impacts of pollinator declines: An approach to assessing the consequences. *Ecology and Society*, 5(1), Article 8. https://doi.org/10.5751/ES-00272-050108

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274, 303–313. https://doi.org/10.1098/rspb.2006.3721
Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Experimental evidence that honeybees deplete wild insect densities in a flowering crop. *Proceedings of the Royal Society B: Biological Sciences*, 283, Article 20161641. https://doi.org/10.1098/rspb.2016.1641

Liu, F., Gao, J., Di, N., & Adler, L. S. (2015). Nectar attracts foraging honey bees with components of their queen pheromones. *Journal of Chemical Ecology*, 41, 1028–1036. https://doi.org/10.1007/s10886-015-0642-2

Łoś, A., Skórka, P., Strachacka, A., Winiarczyk, S., Adaszek, I., Winiarczyk, M., & Wolski, D. (2020). The associations among the breeding performance of *Osmia bicornis* L. (Hymenoptera: Megachilidae), burden of pathogens and nest parasites along urbanisation gradient. *Science of the Total Environment*, 710, Article 135520. https://doi.org/10.1016/j.scitotenv.2019.135520

MacKenzie, K. E., & Eickwort, G. C. (1996). Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L.) in central New York. *Journal of the Kansas Entomological Society*, 69(4), 185–194.

Masierowska, M., & Piętka, T. (2014). Variability in nectar and pollen production in flowers of double-low lines of white mustard (*Sinapis alba* L.) and their attractiveness to honey bees. *Acta Scientiarum Polonorum Hortorum Cultus*, 13(5), 197–209.

Nagy-Déri, H., Orosz-Kovács, Z., & Farkas, Á. (2013). Comparative studies on nectar from two self-fertile and two self-sterile cultivars of quince (*Cydonia oblonga* Mill.) and their attractiveness to honeybees. *Journal of Horticultural Science and Biotechnology*, 88(6), 776–782. https://doi.org/10.1016/j.jhortsbi.2013.11513038

Nepi, M., Grasso, D. A., & Mancuso, S. (2018). Nectar in plant–insect mutualistic relationships: From food reward to partner manipulation. *Frontiers in Plant Science*, 9, Article 2018-01063. https://doi.org/10.3389/fpls.2018.01063

Nicolson, S. W., & Thornburg, R. W. (2007). Nectar chemistry. In S. W. Nicolson, M. Nepi, & E. Pacini (Eds.), *Nectaries and nectar* (pp. 215–264). Springer. https://doi.org/10.1007/978-1-4020-5937-7_5

Palma, L. Young, E. C., Farrell, L. W., Adler, L. S., Milano, N. J., Egan, P. A., Irwin, R. E., & Stevenson, P. C. (2019). Secondary metabolites from nectar and pollen: A resource for ecological and evolutionary studies. *Ecology*, 100(4), Article e02621. https://doi.org/10.1002/ecy.2621

Pereira, A. L. C., Taques, T. C., Valim, J. O. S., Madureira, A. P., & Campos, W. G. (2015). Do floral resources influence pollination rates and subsequent fruit set in pear (*Pyrus communis* L.) and apple (*Malus × domestica* Borkh) cultivars? *Journal of Horticultural Science and Biotechnology*, 90(1), 47–56. https://doi.org/10.1071/jh10017

Pervin, M., Hasnat, M. A., Lim, J. H., Lee, Y. M., Kim, E. O., Um, B. H., & Lim, B. O. (2016). Preventive and therapeutic effects of blueberry (*Vaccinium corymbosum*) extract against DSS-induced ulcerative colitis by regulation of antioxidant and inflammatory mediators. *Journal of Nutritional Biochemistry*, 28, 103–113. https://doi.org/10.1016/j.jnutbio.2015.10.006

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*, 25(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Quinet, M., Warzée, M., Vanderplanck, M., Michez, D., Lognay, G., & Jacquemart, A. L. (2016). Do floral resources influence pollination rates and subsequent fruit set in pear (*Pyrus communis* L.) and apple (*Malus × domestica* Borkh) cultivars? *European Journal of Agronomy*, 77, 59–69. https://doi.org/10.1016/j.eja.2016.04.001

Rhodes, C. J. (2018). Pollinator decline – An ecological calamity in the making? *Science Progress*, 101(2), 121–160. https://doi.org/10.1179/ghptj

Roy, R., Schmitt, A. J., Thomas, J. B., & Carter, C. J. (2017). Review: Nectar biology: From molecules to ecosystems. *Plant Science*, 262, 148–164. https://doi.org/10.1016/j.plantsci.2017.04.012

Schmidt, K., Filep, R., Orosz-Kovács, Z., & Farkas, Á. (2015). Patterns of nectar and pollen presentation influence the attractiveness of four raspberry and blackberry cultivars to pollinators. *Journal of Horticultural Science and Biotechnology*, 90(1), 47–56. https://doi.org/10.1080/14620316.2015.11513152

Scott, Z., Ginsberg, H. S., & Alm, S. R. (2016). Native bee diversity and pollen foraging specificity in cultivated highbush blueberry (*Eriocaceae: Vaccinium corymbosum*) in Rhode Island. *Environmental Entomology*, 45(6), 1432–1438. https://doi.org/10.1093/ee/nvw094

Shackleton, K., Balfour, N. J., Al Toufailia, H., Gaisoski, R., Ir de Matos Barbosa, M., Silva, C. A. d. S., Bento, J. M. S., Alves, D. A., & Ratnieks, F. L. W. (2016). Quality versus quantity: Foraging decisions in the honeybee (*Apis mellifera scutellata*) feeding on wildflower nectar and fruit juice. *Ecology and Evolution*, 6, 7156–7165. https://doi.org/10.1002/ece3.2478
Bożek / Nectar Production in Highbush Blueberry

Solís-Montero, L., Vergara, C. H., & Vallejo-Marín, M. (2015). High incidence of pollen theft in natural populations of a buzz-pollinated plant. *Arthropod–Plant Interactions, 9*, 599–611. https://doi.org/10.1007/s11829-015-9397-5

Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., Wattoz, R., Lognay, G., & Jacquemart, A.-L. (2015). Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie, 46*(1), 92–106. https://doi.org/10.1007/s13592-014-0307-0

Statistics Poland. (2019). *Local Data Bank*. https://bdl.stat.gov.pl

Strzałkowska-Abramek, M. (2019). Nectar and pollen production in ornamental cultivars of *Prunus serrulata* (Rosaceae). *Folia Horticulturae, 31*(1), 205–212. https://doi.org/10.2478/fohort-2019-0015

Sushil, S. N., Stanley, J., Hedau, N. K., & Bhatt, J. C. (2013). Enhancing seed production of three *Brassica* vegetables by honey bee pollination in north-western Himalayas of India. *Universal Journal of Agricultural Research, 1*(3), 49–53. https://doi.org/10.13189/ujar.2013.010301

Szkłanowska, K., Bożek, M., & Wieniar ska, J. (1989). Wartość pszczelarska i owocowanie 11 nowych odmian malin (*Rubus idaeus* L.) [Beekeeping value and fruit crop of eleven new raspberry cultivars (*Rubus idaeus* L.)]. *Pszczelnicze Zeszyty Naukowe, 33*, 77–88.

Thomson, D. M. (2016). Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters, 19*(10), 1247–1255. https://doi.org/10.1111/ele.12659

Winfree, R., Gross, B. J., & Kremen, C. (2011). Valuing pollination services to agriculture. *Ecological Economics, 71*, 80–88. https://doi.org/10.1016/j.ecolecon.2011.08.001

Wrzesień, M., Jachula, J., & Denisow, B. (2016). Railway embankments – Refuge areas for food flora, and pollinators in agricultural landscape. *Journal of Apicultural Science, 60*(1), 97–110. https://doi.org/10.1515/JAS-2016-0004

Xiao, Y., Li, X., Cao, Y., & Dong, M. (2016). The diverse effects of habitat fragmentation on plant–pollinator interactions. *Plant Ecology, 217*(7), 857–868. https://doi.org/10.1007/s11258-016-0608-7

Zhao, G., Li, J., Di, N., & Liu, F. (2014). Nectar phenolics drive cross visits between dimorphic flowers by honey bees. *Journal of Apicultural Research, 53*(4), 489–492. https://doi.org/10.3896/IBRA.1.53.4.14