

DOI: 10.5586/aa.1796

Publication history

Received: 2019-05-28

Accepted: 2019-09-03

Published: 2019-12-19

Handling editorMarcin Zych, Faculty of Biology,
University of Warsaw, Poland**Funding**

This work was supported financially by the Ministry of Science and Higher Education of Poland as part of the statutory activities of the Department of Botany and Plant Physiology, University of Life Sciences in Lublin, Poland.

Competing interests

No competing interests have been declared.

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Citation

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

ORIGINAL RESEARCH PAPER

Nectar secretion and pollen production in *Hyacinthus orientalis* 'Sky Jacket' (Asparagaceae)

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* Email: malgorzata.bozek@up.lublin.pl**Abstract**

Flowering, nectar secretion, and pollen production in *Hyacinthus orientalis* 'Sky Jacket' (Asparagaceae) were studied between 2013 and 2015 in Lublin, SE Poland (51°16' N, 22°30' E). The flowering was weather-dependent. It started at the beginning of April or at the end of the month and lasted 14–24 days. The mass of nectar, sugar concentration in the nectar, nectar sugar mass, anther size, and pollen mass in flowers all depended on the flower position in the inflorescence and differed significantly between the years of study. The greatest mass of sugars and pollen was recorded in low-positioned flowers. On average, *H. orientalis* 'Sky Jacket' produced 1.63 mg of sugars and 3.51 mg of pollen per flower. The floral reward was attractive for *Apis mellifera* and *Bombus* spp., which indicate that the species should be propagated not only for its decorative value but also for supporting pollinators in early spring.

Keywordsnectar; pollen; ornamental plants; insect visitors; *Apis mellifera*; *Bombus* spp.**Introduction**

Primary and secondary floral attractants have evolved to attract pollinators and increase plant reproductive success via the impact on the behavior of insect visitors [1–3]. Indeed, a key role is assigned to flower or inflorescence morphological features (e.g., size, color), and floral rewards (nectar and pollen) [4–7]. Nectar is a sugar-rich aqueous solution with 10% to 75% of sugars [8] which represent the main energy source for insect visitors. The plant–insect relationship is primarily shaped by nectar secretion patterns, the concentration of sugars, nectar sugars mass [9], and nectar amino acid content and composition [4]. The number of insect visits [10,11], the duration of a visit within a flower [12], and pollinator guild [10,13], therefore differ considerably between plant species. Pollen has a double function as a provider of male gametes and it is a source of proteins and other macronutrients for insects [13–15]. The pattern of pollen presentation, its amount and quality, i.e., energy-rich compounds, all impact on the pollinator type and influence the success of pollination [16,17].

Insect pollinators depend on nutrients gathered from the nectar and pollen of various plant species [14]. Currently, the diversity of insect pollinators and their population sizes are in worldwide decline [18–21]. The reasons are complex, e.g., the detrimental effects of chemicals used in agricultural production [22], pathogens and diseases [23,24], habitat fragmentation [25,26], and food deficit, which all derive from the lack of mass-flowering plants [20,27]. In Europe, the flowering plant density is higher in urban areas compared to agricultural areas [28]. The disparities are largely due to differences in quality of habitats between urban and rural areas [29]. High species richness and abundance of forage flora in urban parks [30–34], public and private gardens [35–37], cemeteries [38], railway areas [39] have been evidenced. More importantly, all these green areas can be exploited for propagation of nectar and pollen bee flora. The quantity

of available food resources is one of the factors that influence the attractiveness of the flowers for insect pollinators [11,40,41].

The aim of the present study was to evaluate the nectar and pollen quantity in the early spring ornamental plant *Hyacinthus orientalis* L. 'Sky Jacket', which is popular in garden arrangements.

Material and methods

Study site

Field observations were performed in 2013–2015. *Hyacinthus orientalis* 'Sky Jacket' (Asparagaceae) individuals were grown on experimental plots in a suburban area in Lublin, SE Poland (51°16' N, 22°30' E). The plants were grown in a loess soil with a pH 6–7 in a sunny site.

Study species

Hyacinthus orientalis is a bulb geophyte, native to Southwestern Asia. It was introduced into Europe in the sixteenth century [42]. Currently, diverse cultivars are grown as ornamental plants and are used in various early spring arrangements [43]. The bulb is 3–8 cm in diameter. The plant grows to a height of 20–35 cm. The flowers are arranged in a monopodial inflorescence of the raceme type [44]. Hermaphroditic flowers are fragrant, 2–3.5 cm long. The perianth is tubular and six-lobed. *Hyacinthus orientalis* 'Sky Jacket' has blue flowers.

Flowering and insect activity

The dates of the beginning of flowering and the length of blooming period were recorded in each growing season. The beginning of flowering was determined when 10% of the flowers bloomed, the full bloom period was established when 70–80% of the flowers were in bloom, and the end of blooming if >85% of the flowers exhibited termination. The diurnal pattern of blooming and foraging of insect visitors was recorded. Observations were made for three consecutive days in 1-hour intervals between 7 a.m. and 8 p.m. EET (Eastern European Time). All insect visitors were recorded on each census of observation, which lasted 5 min. The number of flowers per raceme ($n = 20$) was established.

Flower life-span

Before nectar sampling, the length of anthesis was determined. To observe the progress of flowering, buds were randomly marked ($n = 2-3$) on different individual plants ($n = 10$) and the flowers monitored twice a day (8 a.m. and 4 p.m.). The beginning of anthesis was defined as the period when the perianth was sufficiently open to permit entry of insect visitors and the end of anthesis when the perianth began to wilt.

Nectar production

Nectar secretion was gathered using glass micropipettes [45,46]. Tulle isolators (mesh size <1 mm) were applied in the flower bud stage on randomly chosen individual inflorescences which remained bagged until nectar sampling. Nectar was collected separately from lower, middle, and top positioned flowers, three times per season. At each time point, three samples were collected (total number of samples = 81). Each sample had nectar from 11–20 flowers. Total sugar concentration was measured with an Abbe refractometer. The total sugar mass per sample was then calculated. Relevant

calculation also allowed the determination of the amount of sugars produced per flower (mg), per inflorescence (mg), and per unit area (g m^{-2}).

Pollen production

Anthers were collected from unopened flowers ($n = 100$) and inserted into glass containers ($n = 3$) of known weight. The samples were collected separately from lower, middle, and top positioned flowers. The glass containers with sampled anthers were placed into a dryer (ELCON CL 65) at ca. 33°C . Anther size was established based on the dry mass of anthers. Pollen was rinsed from anthers with ether (1–3 mL) and with 70% ethanol (2–8 mL). A binocular microscope was used to check the accuracy of the pollen rinsing from anthers. Pollen production was calculated per flower (mg), per inflorescence (mg), and per unit area (g m^{-2}).

Meteorological factors

Weather data were obtained from a local weather station. Monthly and decade means were compared to long-term data (1951–2010). The precipitation in the fall–winter of 2012/2013 was approximately 70% lower than in the long term. The first months of the year 2013 were colder, whilst in May the mean air temperature was some 20% higher compared to the long-term data. A deep snow layer was recorded in April. In 2014 and 2015, the average air temperatures for February and March exceeded the norm. In April of 2014, the air temperature was almost 25% higher compared to long-term data, whereas in April 2015 the air temperature was near the long-term norm.

Data analysis

The nectar and pollen data are presented as means with *SD* values attached. One-way analysis of variance (ANOVA) was applied to test differences in nectar/sugar amounts, sugar concentration, and pollen production [47]. Post hoc comparison of means was tested by the Tukey HSD test at $\alpha = 0.05$. The analyses were performed using STATISTICA ver. 6.0 (StatSoft Poland).

Results

The flowering of *H. orientalis* 'Sky Jacket' differed considerably between the growing seasons. The first months of the year 2013 were colder compared to the long-term data and therefore blooming started at the end of April and lasted 12 days (Fig. 1). In 2014 and in 2015, blooming commenced earlier, on 8 and 11 of April, respectively, and lasted longer: 19 days in 2015 and 24 days in 2014. Anthesis proved to be weather-dependent.

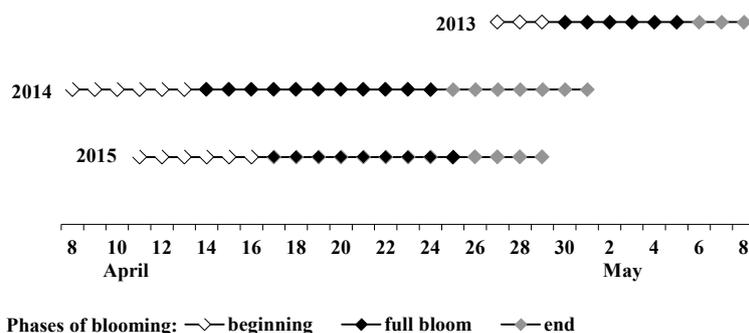


Fig. 1 Time and duration of blooming of *Hyacinthus orientalis* 'Sky Jacket' in 2013–2015.

In 2013, with a average monthly air temperature near to the long-term average, the flower life-span lasted 4–6 days. It was prolonged to 10–12 days in 2014 and 2015, respectively, when sudden drops in air temperature with simultaneous rainfall occurred during blooming. Accordingly, the inflorescence was in bloom from 7–8 days until 14–18 days. Most flowers opened in the early hours with approximately 50% being open up to 10 a.m. (Fig. 2). A year effect was found for the number of flowers per inflorescence. On average, 51.6 flowers were recorded per inflorescence. In 2013, the number of flowers was 45–50% higher than in other years (2013 mean = 65.8, 2014 – 42.9, and 2015 – 46.0 flowers per inflorescence). These differences in the number of flowers per inflorescence between years were statistically significant.

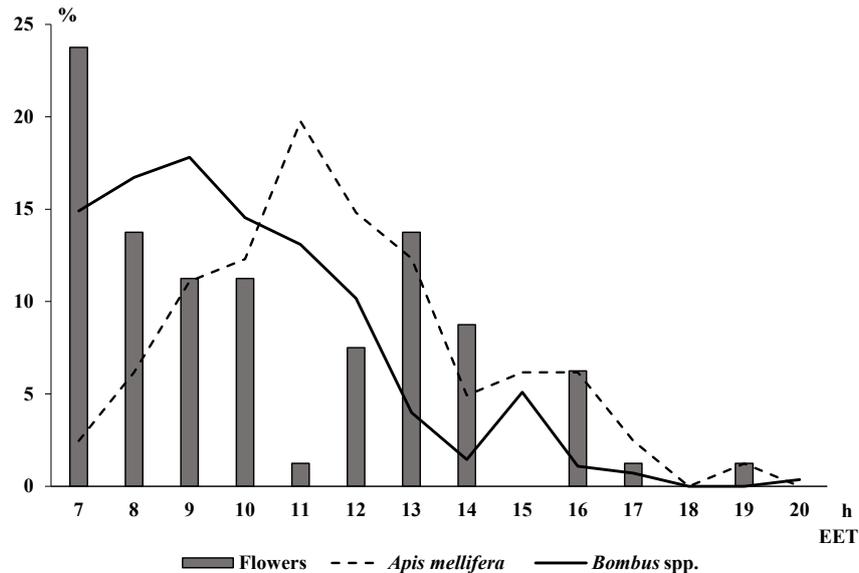


Fig. 2 Diurnal pattern of flowering of *Hyacinthus orientalis* 'Sky Jacket' expressed as the number of flowers opened at 1-h intervals in relation to the total opened during the day and the diurnal activity of insect visitors observed in SE Poland (means calculated from 2013–2015; EET – Eastern European Time).

No nectar was found in the bud stage. The secretion started on the first day of anthesis and lasted until flower wilting. It was found that the amount of secreted nectar depends on the flower position in raceme (Fig. 3); the greatest amount was recorded in low-positioned flowers (mean = 4.7 mg per flower). The nectar sugar concentration also varied depending on flower position; it amounted to 42.6% on average. The quantity of sugars, which depends on nectar amount and sugar concentration was the highest in low-positioned flowers (mean = 2.5 mg per flower). In mid-positioned flowers, the mass of sugars was 25% lower compared to the low-positioned. In top-positioned flowers the mass of produced sugars was 45% lower compared to the low-positioned. The quantity of secreted nectar, nectar concentration, and the mass of produced sugars were year-dependent (Tab. 1). The lowest amount of nectar was produced in 2014 and it was approximately 30–40% lower than in other study years. The sugar concentration in the nectar varied between years (mean = 18.97% in 2013, 66.14% in 2014, and 42.74% in 2015). Accordingly, the lowest amount of sugars was produced in 2013 (only 0.88 mg per flower).

The size of anthers (expressed as anther dry mass) and the amount of pollen produced per flower varied depending on the flower position in the inflorescence and the year. The largest anthers were recorded in the low-positioned flowers (Fig. 4). The greatest amount of pollen was offered in low-positioned flowers, the lowest by the top-positioned (Tab. 2). The average amount of pollen produced per flower was 3.5 mg. The greatest amount of pollen was recorded in 2014 (mean = 3.87 mg). One inflorescence produced 78.7 mg of sugars and 179.7 mg of pollen and would thus deliver 3.46 g of sugars and 7.91 g of pollen per m².

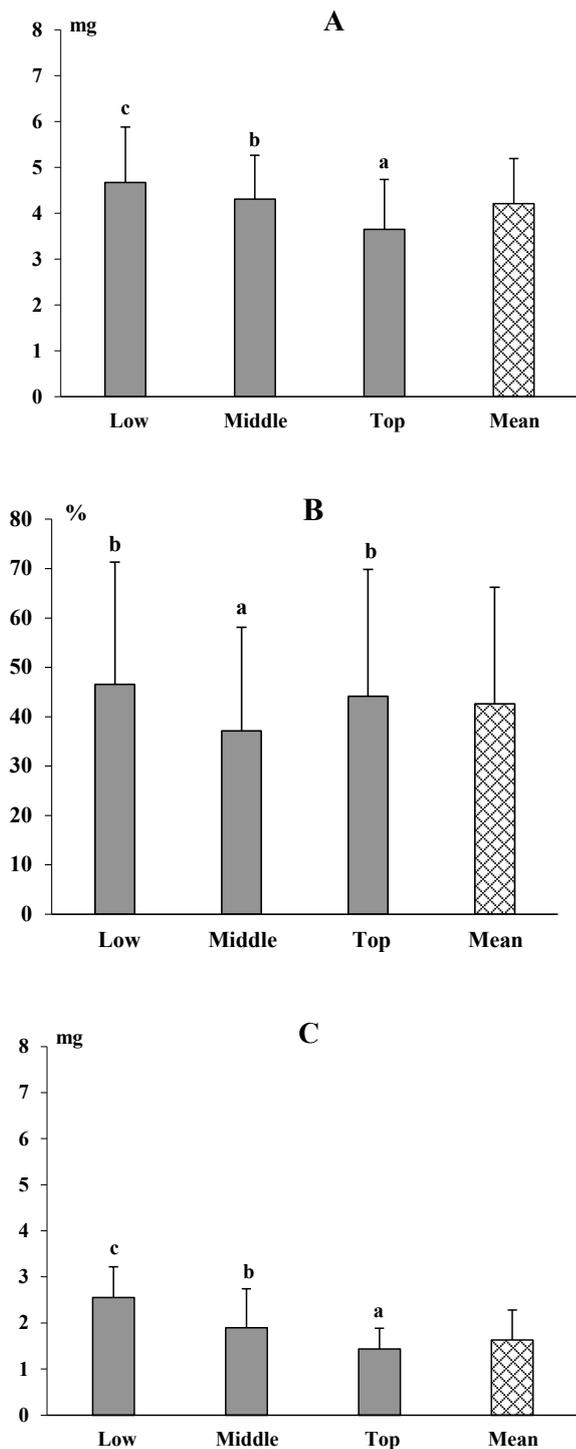


Fig. 3 The amount of secreted nectar (A), the sugar concentration (B), and the mass of sugars per flower (C) depending on the position of the flower in inflorescence of *Hyacinthus orientalis* 'Sky Jacket' (means from 2013–2015).

Both honeybees and bumblebees were observed foraging on flowers (Fig. 2) but no other insect visitors were recorded. Honeybees collected mainly pollen (60–70% of observed workers). Bumblebees visited flowers of *H. orientalis* most frequently in the morning hours (7 a.m.–10 a.m.; 64% of the total number of observed *Bombus* spp.), whereas the peak of honeybee visits occurred between 11 a.m. and 1 p.m. (47% of the total number of *Apis mellifera* L. individuals noticed). No preferences of insect visitors were observed for flower position in an inflorescence.

Discussion

During this study period, the weather parameters showed a contrast between February/March which influenced the disparity in the onset of flowering of *H. orientalis* 'Sky Jacket' between the study years. It is generally accepted that meteorological factors, mainly air temperatures and precipitation, are the main elements that affect the onset and duration of flowering of different plant species [48,49]. In 2014 and 2015, air temperatures in February/March higher than long-term means speeded up the onset of flowering. Conversely, the deep snow layer recorded at the beginning of April 2013 caused a delay of flowering time, which was recorded in the end of April. Such correlations are common and have been reported in other geophytes [48,50].

The mean flower life-span differed considerably between the years of study. When air temperatures dropped and precipitation was higher during blooming, the flower life-span was twice as long (10–12 days) compared to when the air temperature was higher (flower life-span only 4–6 days). This clearly demonstrates the plasticity of the species to weather conditions. The influence of air temperature and precipitation on the flower life-span has been shown for many species, e.g., in *Corydalis* 4 days of disparity in flower life-span was recorded between cold and hot weather [48]. Plastic responses to weather parameters in flowers and flowering can suggest adaptability to increase the probability for pollination by insect pollinators. It is accepted that insect flying activity decreases under low temperature and rainy weather conditions [51].

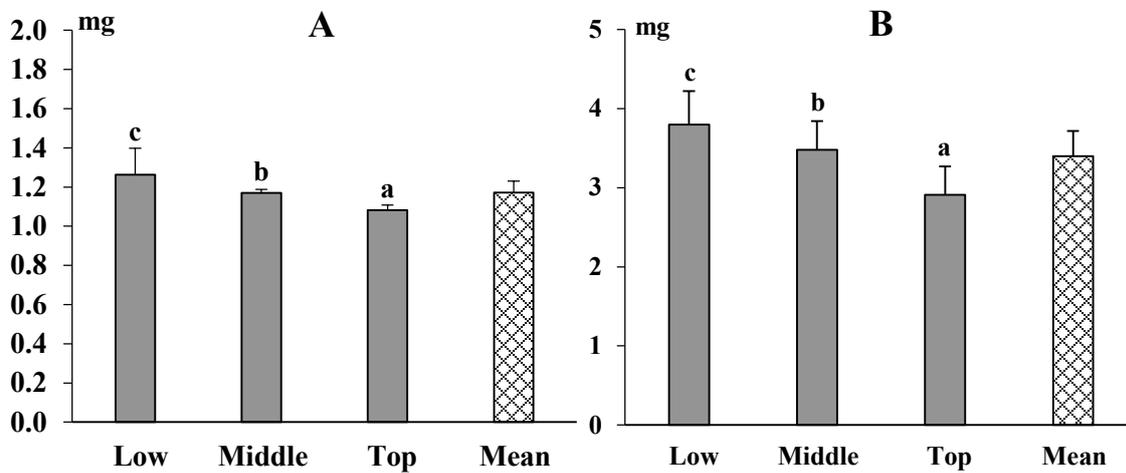
In this study, the amount of secreted nectar, the mass of produced sugars, and pollen production depended on the position of the flower in inflorescence. These results suggest uneven distribution of photosynthesis derivative sugars between flowers. Flower structures are supplied with organic compounds (primarily carbohydrates) and most probably more assimilates are delivered to low-positioned flowers. The impact of the flower position on floral reward quantity was documented by Denisow et al. [52] for *Hosta* 'Krossa

Regal' (Asparagaceae), by Stpiczyńska [53] for *Platanthera chlorantha* (Custer) Rchb. (Orchidaceae), and resource limitation was indicated as the most probable factor for an irregular pattern of nectar distribution. According to Cruden et al. [54], variations in the amount of secreted nectar/sugars may impact on reproduction effects, e.g., by geitonogamy limitation. The resource allocation hypothesis can also explain the differences in nectar production between low-, mid-, and top-positioned flowers. The dependence was shown for *Oenothera* spp. arranged in raceme inflorescence by Antoń and Denisow [49].

Tab. 1 Nectar secretion, sugars concentration in nectar, and total sugar yield in *Hyacinthus orientalis* 'Sky Jacket' in 2013–2015.

| Year | Mass of nectar per flower (mg) | | Concentration of sugars in nectar (%) | | Total sugar yield | | | | |
|------|--------------------------------|------|---------------------------------------|------|-------------------|------|------------------------|-------|-------------------------|
| | Mean | ±SD | Mean | ±SD | Per flower (mg) | | Per inflorescence (mg) | | Per m ² (g)* |
| 2013 | 4.91 ^b | 2.05 | 18.97 ^a | 6.20 | 0.88 ^a | 0.14 | 57.90 | 25.22 | 2.55 |
| 2014 | 3.09 ^a | 1.82 | 66.14 ^c | 9.10 | 2.02 ^b | 0.31 | 86.66 | 16.83 | 3.81 |
| 2015 | 4.63 ^b | 1.28 | 42.74 ^b | 4.30 | 1.99 ^b | 0.18 | 91.54 | 31.30 | 4.03 |
| Mean | 4.21 | 1.72 | 42.62 | 6.53 | 1.63 | 0.21 | 78.70 | 21.51 | 3.46 |

ANOVA procedures were performed separately for each analyzed feature. Means with the same small letter do not differ significantly between years of study, at $\alpha = 0.05$, based on HSD Tukey's test. * Number of bulbs: 44 per 1 m².

**Fig. 4** The dry mass of a single anther (A) and the mass of produced pollen per flower (B) depending on the position of the flower in the inflorescence of *Hyacinthus orientalis* 'Sky Jacket' (means from 2013–2015).**Tab. 2** Size of anthers and the mass of pollen produced in the flowers of *Hyacinthus orientalis* 'Sky Jacket' in 2013–2015.

| Year | Dry mass of anthers per flower (mg) | | Mass of pollen | | | | |
|------|-------------------------------------|------|-------------------|------|------------------------|-------|-------------------------|
| | Mean | ±SD | Per flower (mg) | | Per inflorescence (mg) | | Per m ² (g)* |
| 2013 | 7.17 ^b | 2.15 | 3.38 ^a | 1.32 | 222.40 | 12.81 | 9.79 |
| 2014 | 7.29 ^b | 1.65 | 3.87 ^b | 0.98 | 166.15 | 24.33 | 7.31 |
| 2015 | 6.63 ^a | 2.62 | 3.27 ^a | 2.10 | 150.42 | 21.25 | 6.62 |
| Mean | 7.03 | 2.14 | 3.51 | 1.47 | 179.66 | 19.46 | 7.91 |

ANOVA procedures were performed separately for each analyzed feature. Means with the same small letter do not differ significantly between years of study, at $\alpha = 0.05$, based on HSD Tukey's test. * Number of bulbs: 44 per 1 m².

Year-to-year disparities have been documented for nectar/sugars production. Nectar production depends on diverse factors, notably temperature, relative humidity, light, or ambient CO₂ concentration [55,56]. Environmental factors have been reported to influence nectar/sugar production in many plant species [32,57]. In 2013, the lowest sugar mass per flower was noted. This may be related to short life-span, which indicates a shorter time of activity of nectaries. A similar correlation was found by Denisow et al. for *Corydalis* species [48].

Differences in pollen production were noted between growing seasons which may be related to differences in weather conditions [58,59]. In particular, in early spring/spring plants low air temperatures are reported to decrease the mass of pollen produced in their flowers [48,60]. A deficit of precipitation can considerably limit the mass of pollen produced, which was reported for the Ranunculaceae species *Adonis vernalis* L. [61], *Anemone sylvestris* L. [62], and in Lamiaceae species, *Salvia pratensis* L., *S. verticillata* L., and *Origanum vulgare* L. [11].

The estimated average sugar yield (2.55–3.81 g m⁻²) and pollen yield (6.62–9.79 g m⁻²), indicate that *H. orientalis* 'Sky Jacket' is quite a good forage yielding plant. For example, early spring *Corydalis solida* (L.) Clairv. (Papaveraceae) can produce 0.46–0.52 g m⁻² sugar [48], and *Hosta* spp. (Asparagaceae) can deliver 0.23–1.18 g m⁻² of sugars [63]. *Hyacinthus orientalis* 'Sky Jacket' is also a good pollen-yielding species as the amount of estimated pollen produced per m² is higher than that assessed for *Adonis vernalis* (Ranunculaceae), recognized as a good pollen-yielding plant that can produce 0.3–1.0 g m⁻² pollen [61].

In our study, *Apis mellifera* and *Bombus* spp. were recorded and both nectar and pollen foragers were observed, which indicates that *H. orientalis* 'Sky Jacket' is an attractive source of food for these pollinators. In conclusion, it can be stated that it is worth propagating *H. orientalis* 'Sky Jacket' not only for decorative purposes but also for supporting honeybees and bumblebees in the early spring. Such activity is in accordance with the assumption of strategies developed for insect conservation [18,20,64–67]. The species can be propagated in different kinds of arrangements, in particular in urban areas, such as in private gardens, parks, or for attractive displays of plants in containers.

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Nektarowanie i produktywność pyłkowa *Hyacinthus orientalis* 'Sky Jacket' (Asparagaceae)

Streszczenie

Badania biologii kwitnienia, sekrecji nektaru oraz produkcji pyłku przez kwiaty hiacynta wschodniego (*Hyacinthus orientalis* 'Sky Jacket') prowadzono w latach 2013–2015 w warunkach klimatycznych Lublina. Kwitnienie, w zależności od warunków meteorologicznych, rozpoczynało się na początku lub końcu kwietnia i trwało 14–24 dni. Masa nektaru, koncentracja cukrów w nektarze, masa cukrów w nektarze, wielkość pylników oraz masa pyłku w 1 kwiecie zależały od pozycji kwiatu w kwiatostanie i różniły się istotnie pomiędzy latami badań. Najwięcej cukrów oraz pyłku produkowały kwiaty położone w dolnej części kwiatostanu. Średnia masa cukrów wynosiła 1,63 mg/kwiat, a pyłku 3,51 mg/kwiat. Kwiaty hiacynta wschodniego były odwiedzane przez pszczołę miodną oraz trzmiele. Gatunek ten powinien być propagowany nie tylko ze względu na wartość ozdobną, ale również dla wsparcia bazy pokarmowej owadów zapylających w okresie wczesnej wiosny.