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Nectar and pollen production of *Helianthus tuberosus* L. – an exotic plant with invasiveness potential

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Abstract – In Central Europe, *Helianthus tuberosus* L. is a late summer/autumn bloomer (August/November). The disc florets produce both nectar and pollen. Floral reward is available in male-phase flowers (pollen and nectar) and in female-phase flowers (nectar). The floral reward is attractive to a variety of insect visitors (honey bees, wasps, flies and butterflies). The season of blooming as well as the total sugar yield (25.4 – 47.4 kg ha^{-1}) and pollen yield (57.8 – 212.7 kg ha^{-1}) indicate that *H. tuberosus* is important in the enhancement of food resources for pollinators. The generative reproduction in *H. tuberosus* is impaired (the species does not set seeds/fruits). However, due to its attractiveness for a variety of pollinators in both rural and urban areas, the spread of *H. tuberosus* should be monitored. Moreover, its propagation needs to be attended with restrictions.

Keywords: alien plant, *Apis mellifera*, *Bombus* spp., insect visitors, nectar, pollen

Introduction

Alien plant species can be introduced by animals and/or accidentally or intentionally by humans (Tokarska-Guzik et al. 2010). Such species can spread at a high rate in both urban and rural landscapes due to their biological properties, e.g. anthropochorous and anemochorous dispersal modes and long-term or transient seed banks, and/or recruitment of reproductive offspring (Lockwood et al. 2007, Wrzesień et al. 2016a, Denisow et al. 2017). Over recent decades, the acceleration in the rate of biological invasions has been noted worldwide possibly due to globalization of trade and transport, and climate change (Tokarska-Guzik et al. 2010, Denisow and Malinowski 2016). Many negative impacts of invasive species on native species richness, the composition of local biocoenoses and the functioning of local ecosystems have been recorded (Weber 2003, Tokarska-Guzik et al. 2010).

In particular, the arrival of novel entomophilous plant species in new areas is considered to be harmful for local biocoenoses as it can potentially interrupt plant-insect interactions (Aizen et al. 2008, Stout and Morales 2009). Therefore, there is a growing body of interest in invasive entomophilous species, which can be expected to be visited and pollinated by native insect pollinators (Denisow et al. 2016a). However, the impacts of alien species on pollinators vary according to the floral traits of the plant species (Stout and Tiedeken 2017). In many areas alien plant species are responsible for the reduction of food resources and initiate gaps in food availability (Goulson et al. 2015, Jachuła et al. 2018a, Wrzesień et al. 2016b). On the other hand, several alien species (e.g. *Solidago* spp., *Impatiens grandulifera* Royle) due to their prolific production of nectar sugars per unit area have attracted considerable attention from beekeepers (Guzikowa and Maycock 1986, Brodschneider and Crailsheim 2010).

Helianthus tuberosus L. (Asteraceae), the Jerusalem artichoke or topinambour, is an entomophilous, perennial plant native to eastern North America. The species is attractive to pollinators due to its floral traits (impressive inflorescences, late summer blooming) and the reward offered (CABI 2018). It was intentionally introduced into Europe in the 17th century as an ornamental plant, attractive for its showy, eye-catching inflorescences (CABI 2018). Nowadays, the species is widely cultivated across the temperate and tropical climate regions (Yang et al. 2015). There is an increasing interest in commercial-scale cultivation of *H. tuberosus,* due to needs of the food, cosmetic and pharmaceutical industry (Seiler

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and Campbell 2006). In particular, the inulin gathered in *H. tuberosus* tubers is evidenced to have therapeutic properties being a dietary fiber and known to have prebiotic effects, and enhances the immune system in humans (Ma et al. 2011). The plant is also grown as an energetic plant or good quality feedstuff for animals (Yang et al. 2015). However, the likelihood that it will escape from cultivation and its invasiveness is documented in many regions, in Europe, Asia, New Zealand and South America (CABI 2018; Weber 2003). Further expansion into new areas is expected due to the globalization of transport and climate change (Lockwood et al. 2007, Tokarska-Guzik et al. 2010).

In plant-pollinator interactions, nectar and pollen are the main floral rewards important in establishing a relationship (Antoń and Denisow 2014, Rodríguez-Riaño et al. 2014). Nectar predominately contains sugars and is regarded as a cost-effective (easy to digest and absorb) major energetic floral reward for pollinators (Nicolson and Thornburg 2007). The nectar traits (volume, sugar concentration) vary among species (Chalcoff et al. 2006, Denisow et al. 2016b, Strzałkowska-Abramek et al. 2016a, b, Jachuła et al. 2018c). Nectar production and the sugar concentration are known to be considerably influenced by environmental conditions (Nicolson and Thornburg 2007, Strzałkowska-Abramek et al. 2018).

Pollen also attracts pollinators as it is a major source of proteins and other nutrients (vitamins, lipids, hormones) crucial for a well-composed pollinator diet essential for insect growth and development as well as immunocompetence (Filipiak et al. 2017, Jachuła et al. 2018c). Nectar and pollen traits are recognized to be important for the foraging behavior of pollinators (Pacini and Hesse 2005, Denisow 2011, Antoń and Denisow 2018).

Helianthus tuberosus is a tall perennial plant, 1–2.3 m in height. The plant forms head inflorescences (ca. 3–5 cm in diameter). The heads are composed of outer sterile, bright-yellow ligulate florets and inner bisexual golden-yellow disc florets (Swanton et al. 1992). *H. tuberosus* inhabits areas on moist, nutrient-rich, sandy or loamy soils, especially along rivers, fallows, railway embankments, abandoned fields (Kays and Nottingham 2007, Tokarska-Guzik et al. 2010, EPPO 2014).

The objective of the present study were: (i) to assess the phenology of blooming, (ii) to evaluate nectar and pollen quantity that can be used as food by insects, (iii) monitor the spectrum of insect visitors, and (iv) check the pollination requirements of *Helianthus tuberosus*, an exotic plant in Europe with high invasiveness potential. We also checked if the plant traits and insect visitor composition differ among plant populations grown in an urban and a nearby rural area.

Materials and methods

Study area

The study was made in the years 2014–2015 in two populations of *Helianthus tuberosus* localized in the Lublin Upland, SE Poland (51°08'–51°18'N, 21°27'–21°41'E; elevation: 170–220 m a.s.l.). The first population was grown in an urban area, the second in a rural area in the vicinity. The urban site was localized in Lublin, the largest city of south-eastern Poland, with flora characteristic specific for cities with a so-called atmospheric urban heat island (UHI) (Rysiak and Czarnecka 2018). The average annual air temperature was lower in the rural than in the urban area – in 2014 by 0.8 °C and in 2015 by 1.3 °C.

The experimental plots of the urban site (approx. 10 m^2 each; n = 3) were established on ruderal spaces located close to built-up areas. The rural plots (approx. 10 m^2 each; n = 3) were localized in a zone adjacent to the urban area. The rural area is characterized by ongoing residential development, however agricultural production is still evolving. The distance between the experimental plots localized in both the urban and the rural area was approximately 10 km.

Flowering observations

The flowering phenology was monitored at each study site. We visited the study populations every 3–7 days and recorded the onset (= beginning), peak (= full bloom), and the end (= termination) of blooming (Denisow et al. 2014). The beginning of blooming was defined by 10% of inflorescences per individuals in bloom, full bloom was indicated if ca. 50% of the inflorescences were in bloom, and the end of blooming was identified when 80% of inflorescences on individuals had completed flowering. In each population, 10 individuals were randomly selected for phenological observations.

The duration of the male and female phases, life-span of disc florets (n = 20 disc florets per population, per year) and individual inflorescences (n = 10 heads) were assessed. The observations were made at 1-hour intervals. The male phase was recognized from the beginning of pollen presentation to the beginning of opening of stigma lobes. The female phase was defined as a period between opening of stigma lobes and corolla wilting. The duration of inflorescence life-span was recorded by marking the inflorescences with just opened disc florets. These inflorescences were followed until the end of last floret blooming. The disc floret life-span was defined as the period from the time when the flower bud was opened to its ending when the corolla was shed.

We established the density of shoots in each population. The shoots were counted in 6 randomly selected areas of 1 m^2 (frame method, Denisow 2011). The total number of florets per unit area was calculated by multiplying the number of heads per shoot (n = 20–30 per year per population) with the average number of disc florets per head (n = 30 per year per population) and with the number of individual shoots.

Nectar and pollen production

Nectar production was assessed using capillary pipettes (Stpiczyńska et al. 2014). Prior to nectar collection, we excluded insect visitors from entire head inflorescences (n = 10–20) using tulle isolators. Sampling of nectar was attempted at 4 different time points of the blooming period (between 20th August and 1st October). At each time 3–9 samples (from 20–30 disc florets) were collected. Nectar was collected in previously weighed micro-capillary pipettes. The nectar mass was assessed reweighting the pipettes with collected nectar (WPS-36 analytical balance; RADWAG, Poland). Sugar concentration was established with Abbe refractometer (RL-4 PZO, Warsaw, Poland). Then the total sugars mass was calculated for florets (in mg), head inflorescences (mg), and for unit area (kg ha^{-1}).

Pollen production was evaluated using the ether-ethanol method (Denisow 2011). We extracted the buds of disc florets from head inflorescences. Unopened anthers from buds were collected in weighed glass containers (250 anthers per trial × 4 replications). Next, the glass containers with anthers were placed into a dryer (ELCON CL 65) at ca. 33 °C. The pollen was rinsed from anthers once with pure ether (1–2 ml) and then 4–6 times with 70% ethanol (10–20 ml). The mass of produced pollen was calculated per disc floret (in mg), per head inflorescence (in mg), per stem (in g), and per 1 ha (in kg).

Pollination requirements and insect visitors

We checked the fruit/seed set using different pollination treatments, i.e. (i) open pollination – with free access of insect visitors to flowers, (ii) self-pollination – with exclusion of insect visitors by bagging flowers with tulle isolators, (iii) artificial cross-pollination – flowers open-pollinated and additionally hand-pollinated with pollen collected from flowers of other individuals.

Simultaneously with the blooming observations, we recorded the pattern and intensity of insect visits. The observations were made at the same time and were conducted for two days at one week intervals (6 days of observations for each site, in total). Insect foraging at 8.00, 12.00 and 18.00 h (GMT + 2.00 h) was noted. During each census of observation, the total number of visiting insects was recorded. The following categories were determined: 1. *Apis mellifera*, 2. *Bombus* species, 3. other Hymenoptera (solitary bees), 4. *Vespula* species 5. Diptera, 6. Syrphidae, 7. Lepidoptera, 8. Coleoptera.

Data analysis

Means of data measured at urban and rural sites and in different years were compared with one-way ANOVA with Tukey's multiple comparisons test. For statistical evaluation of the results, the Statistica software ver. 6 (Statsoft, Poland, 2001) was used.

Results

Flowering and floral morphology

Helinathus tuberosus bloomed in August-November with a full bloom in late August (2015) and early-mid September (2014). Each year the start of blooming was noted earlier (9–14 days) in the urban (site A) than in the rural landscape (site B). In a single head, the flowering starts from the outer disc florets. Anthesis of the ray florets occurred in the morning (7.00–9.00 GMT+2 h). Furthermore, the diurnal opening of disc florets was documented and the process was most intensive in the early afternoon (15.00–18.00 GMT+2 h). The inflorescence life-span ranged from 5.6 to 9.3 days (mean = 7.4 days).

The length of corolla tube in disc florets ranged between 3.57 and 4.88 mm. Neither population nor the year affected the disc florets' length. Disk florets are protandrous, therefore three stages of floret development can be distinguished from the edge of the inflorescence towards the inner part, i.e. (i) male disc florets presenting pollen and offering nectar, (ii) female disc florets with nectar available, and (iii) immature buds.

The study populations differed in the number of developed disc florets per inflorescence and heads per stem (Tab. 1). Individuals of *H. tuberosus* in the urban population produced fewer (ca. 12%) flower heads, bearing fewer disc florets (ca. 6%) than the individuals in the rural population. Interpopulation variation in plant density was noted. The density of the stems of *H. tuberosus* varied over the study period only in the urban site.

Nectar and pollen rewards

Nectar production began in 1-day disc florets and lasted 3–5 days in individual flowers of *H. tuberosus*. The nectar was available till the end of anthesis. The amount of secreted nectar was significantly higher in disc florets of the rural population than in those of the urban population ($F_{1,15}$ = 8.589, P = 0.011) (Tab. 2). Year-to-year disparities

Tab. 1. Dates of flowering, duration of blooming stages and blooming abundance of *Helianthus tuberosus* in 2014–2015 in urban and rural sites, Lublin Upland, SE Poland. Means ± SD (standard deviation) are presented. Means followed by the same small letters are not significantly different between years and means followed by the same capital letters are not significantly different between study sites, at α = 0.05 based on Tukey's test.

Site	Year	Flowering period	Duration of flowering (days)	Number of disc florets per head	Number of heads per stem	Number of disc florets per stem (thous.)	Number of stems per m^2
Urban	2014	10 August – 2 November	85	118.4±27.5^a	23.2±9.3^a	2.7±0.8^a	42.8±15.6^b
	2015	20 July – 20 November	124	120.2±31.6^a	29.4±2.7^b	3.5±0.5^b	24.5±7.8^a
	mean		104.5	119.3±14.9^A	26.3±6.8^A	3.1±0.8^A	29.7±10.5^A
Rural	2014	19 August – 12 November	86	129.8±11.6^a	29.8±1.8^a	3.8±0.5^a	39.7±0.5^a
	2015	04 August – 03 November	92	123.6±13.5^a	28.5±2.0^a	3.5±0.6^a	39.8±0.4^a
	mean		89.0	126.7±12.8^B	29.2±2.0^B	3.7±0.6^B	39.8±0.4^B

Tab. 2. Nectar production, sugar concentration and sugar mass in *Helianthus tuberosus* in 2014–2015 in urban and rural sites, Lublin Upland, SE Poland. Means ± standard deviation are presented. Means with the same small letter do not differ significantly between study seasons within sites, whereas means with the same capital letter do not differ significantly between study sites at α = 0.05, based on Tukey's test.

Site	Year	Nectar amount per disc floret (mg)	Sugar concentration (% w/w)	Sugar amount per disc floret (mg)	Sugar amount per head (mg)	Sugar amount per stem (g)
Urban	2014	0.053±0.012[a]	39.0±8.9[a]	0.021±0.011[a]	2.49±1.58[a]	0.057±0.022[a]
	2015	0.062±0.015[b]	48.8±6.9[b]	0.030±0.016[b]	3.61±2.65[b]	0.105±0.034[b]
	mean	0.058±0.021[A]	43.9±10.3[B]	0.026±0.013[A]	3.05±2.15[A]	0.081±0.051[A]
Rural	2014	0.079±0.017[a]	32.5±3.6[b]	0.026±0.012[a]	3.37±2.95[a]	0.099±0.027[a]
	2015	0.145±0.012[b]	26.8±7.2[a]	0.039±0.145[b]	4.82±3.58[b]	0.137±0.065[a]
	mean	0.112±0.015[B]	29.7±5.8[A]	0.033±0.089[B]	4.10±3.74[B]	0.118±0.054[B]

in the amount of produced nectar were also recorded ($F_{1,15} = 7.64$, $P = 0.004$). On average, sugar nectar concentration amounted to 29.7% at the rural site, while nectar in the urban site was more concentrated. The nectar sugar mass varied among populations ($F_{1,15} = 13.619$, $P = 0.004$) and years of study ($F_{1,15} = 3.752$, $P = 0.037$). The total mass of sugar per disc floret was 0.029 mg, on average. The head inflorescences of rural population produced 35% more sugars than the urban population.

In *H. tuberosus*, the disc florets are protandrous. During sunny days, the dehiscence of anthers started just after opening of the floret and pollen was available to insects for 1–2 days, if the air temperature was > 20 °C. The pollen presentation lasted 3–4 days, if the air temperature was < 15 °C. A significant population effect ($F_{1,15} = 4.067$, $P = 0.041$; Tab. 3) and a year effect ($F_{1,15} = 11.808$, $P = 0.048$) were found for the amount of pollen produced per disc floret. The average mass of pollen produced was 0.11 mg per disc floret in 2014 and 0.07 mg per disc floret in 2015. The mass of pollen produced in disc florets of the urban population was 60% lower than in rural population florets.

The total sugar and pollen yield varied in the urban and rural populations (Fig. 1). *Helianthus tuberosus* produced 47.3 kg ha^{-1} of nectar sugars in the rural and 25.4 kg ha^{-1} in the urban area. The pollen productivity was 212.7 kg ha^{-1} of pollen in rural and 57.8 kg ha^{-1} in urban environments, on average.

No set of seeds/fruits was observed in any of the treatments applied.

In *H. tuberosus,* head inflorescence is a unit of attraction for insect foragers. Numerous insects foraged the florets. The spectrum of insect visitors was similar in urban and rural habitats (Fig. 2). However, the proportion of insect visitors differed. A higher proportion of syrphids was observed for-

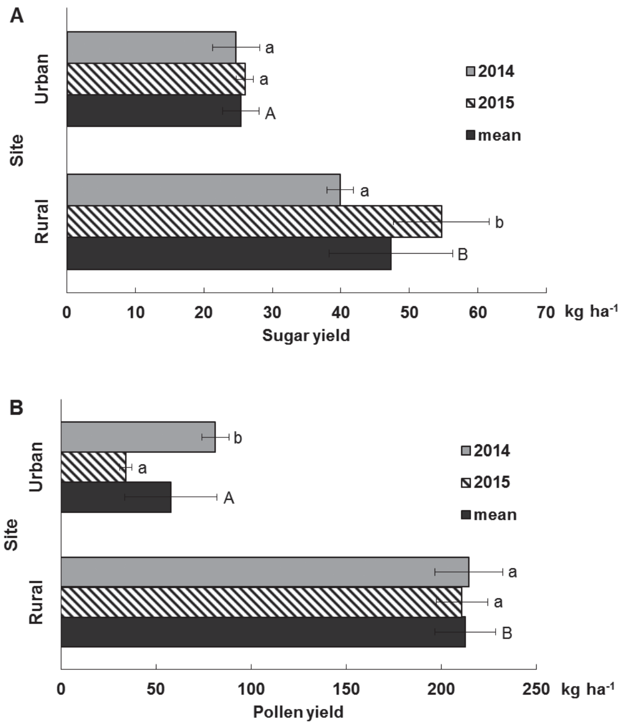

Fig. 1. Sugar (A) and pollen (B) yield of *Helianthus tuberosus* in 2014–2015 in urban and rural sites, Lublin Upland, SE Poland. Means ± standard deviation are presented. Means with the same small letter do not differ significantly between study seasons within sites, whereas means with the same capital letter do not differ significantly between study sites at α = 0.05, based on Tukey's test.

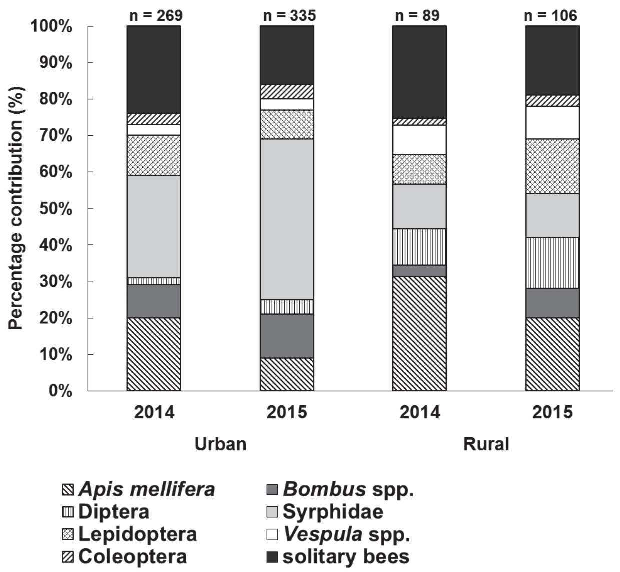

Fig. 2. Spectrum of insect visitors in *Helianthus tuberosus* in 2014–2015 in urban and rural sites, Lublin Upland, SE Poland. Percentage relation of each group of insects to the total number of insect visitors (n) noted is shown.

Tab. 3. The mass of pollen produced per disc floret, per head, and per stem of *Helianthus tuberosus* in the years 2014–2015 in urban and rural sites, Lublin Upland, SE Poland. Means ± standard deviation are presented. Means followed by the same small letters are not significantly different between years and values followed by the same capital letters are not significantly different between study sites, at α = 0.05 based on Tukey's test.

Site	Year	Mass of pollen per disc floret (mg)	Mass of pollen per head (mg)	Mass of pollen per stem (g)
Urban	2014	0.07±0.02[b]	8.29±3.24[b]	0.19±0.08[a]
	2015	0.04±0.01[a]	4.81±1.61[a]	0.14±0.03[a]
	mean	0.06±0.01[A]	6.55±2.89[A]	0.17±0.04[A]
Rural	2014	0.14±0.04[a]	18.17±3.62[a]	0.54±0.35[a]
	2015	0.10±0.07[a]	18.54±7.31[a]	0.53±0.18[a]
	mean	0.12±0.06[B]	18.36±8.48[B]	0.54±0.22[B]

aging on *H. tuberosus* in the urban habitat. Honey bees were more frequently noted in rural plants than in urban. Approximately 3-fold more insect visitors were noted in the urban habitat. Honey bees foraged for nectar and pollen, while wasps, flies, and butterflies foraged for nectar.

Discussion

In SE Poland, *Helianthus tuberosus* is a late summer/autumn bloomer. A similar blooming season has been reported from North America and other European countries (CABI 2018, Yang et al. 2015). Our short–term study indicated that the blooming season of *H. tuberosus* differed in urban and rural areas. In both study years, the species started to bloom earlier in the urban than in the nearby rural zone. The acceleration of flowering in urban compared to rural areas was noted in diverse European regions for a variety of species (Kasprzyk 2016, Stępalska et al. 2016). The prolongation of the flowering season within cities was also documented (e.g., in the largest cities in Britain), as compared to rural surroundings (Dallimer et al. 2016). It is accepted that phenological processes are affected by diverse weather factors (e.g., air temperature, humidity, insolation) (McKinney 2008, Masierowska 2012). In compact built-up areas of many cities higher temperatures than in neighboring areas are evidenced, a phenomenon referred to as an urban heat island (UHI) (Taha 1997). The UHI phenomenon is evidenced in Lublin city and is well-known to have an impact on the vegetation (Rysiak and Czarnecka 2018). However, in addition to microclimatic factors, plant phenology can be modified in relatively close areas by disease/pest occurrence, soil nutrients, or soil water availability (Menzel et al. 2008). We did not observe plants affected by disease/pests in our study plots, and therefore we assume that the difference in the flowering of *H. tuberosus* in the study plots was determined by weather-related factors. In particular, a higher average air temperature was noted in urban areas.

In our study, disparities in flowering abundance (i.e., the number of disc florets per head, head inflorescence per shoot) and quantitative traits of floral reward were evidenced between populations. We assume that the UHI environmental conditions (higher temperature, lower humidity) impacted on plant species phenotypic traits and impaired the number of developed disc florets and inflorescences.

The flowers of *H. tuberosus* are arranged in head inflorescence, which is a characteristic trait of Asteraceae (Wist and Davis 2006, Czarnecka and Denisow 2014). It is suggested that outer ray florets attract pollinators visually, while the inner disc florets' function is to reward the pollinators with food (Wild et al. 2003). In disc flowers of *H. tuberosus,* floral reward is available in male-phase flowers (pollen and nectar) and in female-phase flowers (nectar). Such a pattern of insect visitor-rewarding is commonly found in Asteraceae plants (Hadisoesilo and Furgala 1986, Wist and Davis 2006, Czarnecka and Denisow 2014).

Protandry is a trait characteristic for the Asteraceae family (Howell et al. 1993, Ladd 1994) and is reported to be an adaptation to cross-pollination. Although the disc florets were willingly visited by diverse groups of pollinators, seeds/fruits were obtained neither in open-pollination nor in the self-pollination treatments applied. In its natural range, *H. tuberosus* is recognized as highly self-incompatible species that requires cross-pollination for seed production (Kays and Nottingham 2007). However, poor seed set has been reported, i.e. fewer than 5 per head inflorescence (Swanton et al. 1992). This strategy seems to be reasonable for a plant species that is propagated vegetatively and impaired generative reproduction in *H. tuberosus* does not restrict its effective spread to natural habitats.

Interpopulational differences in nectar production and nectar sugar concentrations were found. Moreover, in each population differences in nectar traits were observed between growing seasons. The variability in the nectar amount produced in flowers is quite common and has been reported among plant species, plant populations or even among individual flowers (Nicolson and Thornburg 2007, Denisow et al. 2014). Nectar production is a complex physiological process dependent on variable environmental factors, i.e. temperature, relative humidity, light, CO_2 concentration, or physico-chemical soil properties (Petanidou and Smets 1996). Habitat/environment conditions were found to have an impact on nectar/sugar production in many plant species, e.g. in *Linaria vulgaris* (Jachuła et al. 2018b), *Lamium maculatum* and *Ajuga reptans* (Mačukanović-Jocić et al. 2004, Jarić et al. 2010) or *Allium ursinum* L. ssp. *ucrainicum* (Farkas et. al. 2012). Nectar production can also be affected by soil nutrient availability or fertilizer application (Denisow et al. 2016a).

In our study, approximately 2-fold more nectar was produced in disc flowers of *H. tuberosus* grown in the rural than in the urban habitat. The rather diluted nectar in flowers at the rural site can be explained by the more humid microclimate conditions associated with rural habitat (located closed to the woodland). On the contrary, the drier microclimate at the urban site may be a background for higher sugar concentration in the nectar.

In our study, the pollen production per flower, per head and per unit area differed between populations (i.e., between rural and urban sites). Disc florets of the urban population produced *ca.* twice as little pollen as those of the rural habitat. Pollen potential of rural plants was almost 3-fold higher. The disparity in pollen production between plant populations may be related to differences in environmental conditions. In particular, a water deficit and air temperatures that exceed the norm is known to impair the mass of pollen produced in anthers (Hedhly et al. 2009, Denisow 2011). Such environmental conditions are probably associated with an UHI (Rysiak and Czarnecka 2018).

The estimated sugar yield 25.4 – 47.4 kg ha^{-1} and pollen yield 57.8 – 212.7 kg ha^{-1}, indicates that *H. tuberosus* may be considered a good forage-yielding plant. The floral reward in *H. tuberosus* was attractive to insect visitors. The availability of food resources in *H. tuberosus* flowers is important to enhance food for pollinators during late summer time, i.e. in a period of poor resources for pollinators. In particular, the pollen available in *H. tuberosus* is very important in the late season and can enhance the overwintering of bee colonies and their strength in spring (Di Pasquale et al. 2016). The pollen produced in *H. tuberosus* was attractive to a variety of pollinators and not just *Apis mellifera.* The fact underlines the importance of the plants in the maintenance of general insect biodiversity.

In conclusion, the season of blooming (late summer/autumn), high nectar and pollen production as well as attractiveness of the reward for insect visitors indicate that *H. tuberosus* is important to enhance food resources for pollinators. However, due to the invasiveness potential of *H. tuberosus*, the species should be propagated with caution.

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