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NECTAR PRODUCTION IN SEVERAL *Campanula* SPECIES (CAMPANULACEAE)

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ABSTRACT

The flowering, nectar production and sugar content were examined in 2012–2013 seasons for three *Campanula* species (*C. persicifolia* L., *C. glomerata* L., *C. trachelium* L.). The flowers of all studied *Campanula* spp. are distinctly protandrous; most of them opened between 10.00 and 14.00; only the flowers of *C. glomerata* continued the opening process until 16.00 (GMT + 2 h). The flower life-span differed between species and was the longest for *C. persicifolia – ca.* 5.5 days and lasted 3.0–3.5 days in *C. glomerata* and *C. trachelium*. The duration of the male phase was 2–3 fold shorter (*C. persicifolia* and *C. glomerata*) than the female phase or was equal (*C. trachelium*). Irrespective of the year of study and the species, the female-biased nectar production pattern was evidenced. The amount of nectar accumulated at the female phase reached 70–87% of the maximum nectar produced by a flower. The total sugar yield (0.4–12.2 g/10 m^2) established for the studied species is low compared to other herbaceous meadow species. However, due to diverse insect visitors groups, the *Campanula* flowers can be recommended to support pollinators in home gardens or on idle lands.

Key words: floral longevity, dichogamy, male phase, female phase, pollinators conservation, bee pastures

INTRODUCTION

In terms of agriculture and horticulture, pollinators provide an essential service, as they pollinate at least 75% of crops [Potts et al. 2010]. Plant-pollinator mediated interactions are also essential for maintenance of entomophilous wild plants grown worldwide [González-Varo et al. 2013]. The decline of pollinators have been evidenced in Europe and North America, therefore their conservation is among principle targets for sustaining flora biodiversity, ecosystem function, and food stability for humans [Kleijn and Langevelde 2006]. Food shortage and nutritional deficiencies are listed among the reasons for global pollinator decline [Alaux et al. 2010, Filipiak and Weiner 2017]. Shortage of floral food resources, i. e. nectar- and pollen-yielding plants, both in space and time, is a result of habitat fragmentation, agriculture intensification, industrial and urban development [Potts et al. 2016]. One of the recommendations to counteract 'pollination crisis' is to restore food niches for pollinators [Fussell and Corbet 1992, Biesmeijer

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et al. 2006, Denisow and Wrzesień 2007, González-Varo et al. 2013]. Nectar- and pollen-yielding plants can be used to improve diversity and population size of pollinators. Therefore, the interest in plant species suitable as food for pollinators is increasing [Denisow et al. 2014, Denisow and Wrzesień 2015, Hicks et al. 2016]. Number of studies have shown that traits of floral rewards (the quantity and quality) impact on insect visitors rate [e.g. Kapyla 1978, Denisow 2005, Pacini and Nepi 2007]. The data on plants that contain an abundance of nectar and pollen, and bloom in succession through the spring and summer seasons may be advantageous for pollinator conservation [Baldock et al 2015].

The representatives of the genus *Campanula* are mainly distributed across the regions of the Northern Hemisphere [Kovacic 2004]. In our previous study we evaluated the pollen production in several *Campanula* species [Denisow and Wrzesień 2015]. The *Campanula* flowers are typically entomophilic and attract diverse floral visitors, i.e. pollen-generalists and pollen specialist species, and nectar-feeding insects [Kapyla 1978, Cresswell and Robertson 1994, Blionis and Vokou 2001, Denisow et al. 2014, Denisow and Wrzesień 2015]. Nectar production in *Campanula* species has not been adequately studied; the data apply to only few *Campanula* taxa [Kapyla 1978]. Nectar is a sugar-rich liquid, an important energy source for diverse insect groups, therefore nectar secretion is one of the most important issues for plant-insect relationship [Denisow 2005, Pacini and Nepi 2007].

The selection of plants for nutritionally useful bee pastures requires the detailed study of flowering, and the nectar and pollen production of different entomophilous species. The present work was undertaken to study nectar production in three *Campanula* species addressing the following questions: Does the nectar production differ between floral sexual phases?, and, What is the amount of produced sugars per flower and the total sugar yield available for pollinators?

MATERIAL AND METHODS

The observations were conducted in 2012–2013 seasons. The perennial herbaceous plant species from the genus *Campanula* (Campanulaceae) were selected for the detailed observations of flowering and nectar production: (i) *Campanula persicifolia* L., (ii) *Campanula glomerata* L., and (iii) *Campanula trachelium* L. (fig. 1A–C). The species were grown at the edge of railway lines within Lublin area (51°16'N, 22°30'E, 210 m a.s.l.), the Lublin Upland, Poland. The *C. persicifolia* occurred on sandy-gravel soil, in plant community of *Epilobietea angustifolii* class; *C. glomerata* on sandy-breakstone soil within meadow of *Molinio-Arrhenatheretea* class, and *C. trachelium* on sandy-loamy soil at the margin of dry-ground forest of *Tilio-Carpinetum*.

Flowering observations were made to establish the phenology of blooming and to determine the number of produced flowers. We used the method described by Denisow [2009] and ascertained the duration of flowering. The initial phase of blooming was recorded when 10% of flowers in the population were in bloom, the full bloom phase when 50–80% of flowers were in bloom, while the end of flowering phase was evidenced when 70–80% of flowers finished flowering.

In maximum blooming phase we marked 5–7 unopened buds, randomly chosen. Every day throughout flower development we observed changes and established floral longevity and duration of male and female phases, the position and dehiscence of anthers. To assess the sexual phases we followed the procedures described by Dafni [1992]. The beginning of anthesis were defined as the time when petals opened enough to allow pollinator to enter the flower and the end of anthesis as the time when petals wilted. The male phase was the period between the beginning of anthers dehiscence through presentation the pollen on the trichomes of presenter and the beginning of stigma lobes opening. Functional female phase with stigma receptivity was the time from stigma opening till anthers wilting. Stigma receptivity was checked using 30% H_2O_2 (n = 5–8 per species, per year). Receptive stigmas have characteristic bubbling observed on their surface when placed in H_2O_2 [Dafni 1992]. The features of flowers morphology were observed using stereo-microscope NIKON SMZ 800.

Abundance of flowering was evidenced for each population as such data are required for calculating the total sugar yield produced per unit area. We counted all buds, flowers and capsule fruits to assess the number of flowers developed per stem of diverse individuals (randomly selected; *n* = 7–12 per species). The density of individuals were established on the basis of 0.1 m^2 circular areas. We made throws (*n* = 7–10) using a circular frame (36.7 cm in diameter) and established the number of flowers per 10 m^2.

The amount of produced nectar was established measuring randomly chosen, unvisited flowers in two flower phases: (i) male and (ii) female. We excluded potential floral insect visitors by bagging inflorescences (n = 10–15 per species, per year) from different individuals (n = 5–8 per species, per year) in tulle isolators (mesh size <1mm). The flowers that reached the appropriate sexual phase were picked out (usually in late morning/mid-day hours; 10.00–12.00), and within a half an hour were transported to the laboratory. The nectar was collected from flowers with glass pipettes of known mass. The mass of nectar (in mg) was determined using an analytical balance (RADWAG, Radom, Poland). Sugar concentration (in %) was established with an Abbe refractometer. The total sugar mass produced per flower (in mg) and then per 10 m^2 (in g) was calculated from the amount of nectar and sugar concentration [Jabłoński 2000].

Statistical analyses. The results are presented as mean values and standard deviations (SD). The analysis of variance (ANOVA) was applied, to find out if there are inter- and intra- specific differences in the mean values of the analysed criteria (nectar mass, nectar concentration, sugar mass) among species and years of study, and among flower age. *Post hoc* comparison of means was tested by the HSD Tukey test [Stanisz 2007]. The level of statistical significance to measure the differences between means for all the analyses was at $\alpha = 0.05$. Statistica software version 6 was applied for these analyses (Statsoft, Krakow).

RESULTS

The flowering of *Campanula* species lasted from the end of May till the second decade of August (tab. 1). The flowering period in the season and flowering duration differed slightly between populations. The species differed in the number of flowers per individual, the lowest number of flowers was indicated for *C. persicifolia*, 3–5 fold more flowers was established for *C. glomerata* and *C. trachelium*. The number of flowers recorded per individual differed between the years of study. Similarly, the year effect was found for the total number of flowers per unit area, which was 2–4.5 times higher in 2013 than in 2012.

Table 1. Phenology of flowering and abundance of blooming of *Campanula* species studied in 2012–2013

Species	Year	Flowering		Number of flowers per individual			Number of flowers per 10 m^2 in thous.		
		date	length (days)	mean	±SD	V (%)	mean	±SD	V (%)
C. persicifolia	2012	30.05–10.07	42	8.2_b	7.8	95.1	0.4	0.3	75.0
	2013	03.06–05.08	64	6.1_a	4.9	80.3	1.6	0.7	43.8
	mean		53	7.2_A		88.9	1.2		50.0
C. glomerata	2012	15.06–10.08	57	16.9_a	5.2	30.8	0.8	0.2	25.0
	2013	01.07–20.08	51	28.4_b	4.1	14.4	3.6	1.1	30.6
	mean		54	22.7_B		20.7	2.2		29.5
C. trachelium	2012	10.07–10.08	32	28.8_a	4.4	15.3	1.4	0.5	35.7
	2013	19.06–15.08	58	39.7_b	3.7	9.3	2.9	0.4	13.8
	mean		45	34.3_C		11.8	2.2		20.9

Mean values ±SD are given. Means within columns with the same small letter do not differ significantly between years within a species and means with the same capital letter do not differ significantly between species based on Tukey's test at $\alpha = 0.05$

Fig. 1. Habitat of A – *Campanula persicifolia*, B – *C. glomerata*, C – *C. trachelium* at the full bloom; D – stages of the development of *C. glomerata* I – bud, II – male-phase flower, III – neutral-phase flower, IV – female-phase flower

Table 2. The duration of total flowers life-span and male and female phases of *Campanula* species

Stage	*C. persicifolia*		*C. glomerata*		*C. trachelium*		Mean for the phase
	mean	± s.d.	mean	± s.d.	mean	± s.d.	
Life-span (days)	5.5_b	1.4	3.5_{ab}	0.6	3.0_a	0.7	4.0
Male phase (days)	2.0_a	0.3	0.9_a	0.3	1.5_a	0.8	1.5_B
Female phase (days)	3.5_b	1.3	2.6_{ab}	0.3	1.5_a	0.5	2.5_A

Values are means from 2012–2013. Morphological definitions of the phases are given in the text. Means within the rows indicate differences between species and if are followed by different small letters are significantly different at α = 0.05 according to Tukey's test. Means indicated with capital letters show differences between flower stages at α = 0.05 according to Tukey's test

Flowers of *Campanula* spp. are arranged in inflorescence and are day-opening. Most flowers opened between 10.00 and 14.00; only the flowers of *C. glomerata* continued the opening process until 16.00 (GMT + 2 h). The bell-shaped flowers of all studied *Campanula* spp. are distinctly protandrous, therefore the number of functionally female flowers increases during the advance of flowering of the individuals and population. At the bud stage, the anthers are rigid and form narrow tubes. The closed lobe formation is centrally positioned with the anthers touching the style closely (fig. 1D). Irrespective of the species, some anthers dehisced in the well-developed buds and the male phase begun before the corolla opening. Pollen release begins in the apical parts of the anthers and sticky pollen covers trichomes present on the style. Flowers of *C. persicifolia* and *C. glomerata* spent less time on anther dehiscence and pollen presentation than on stigma presentation (paired df = 1, F = 0.42, p = 0.001; tab. 2). In *C. trachelium*, both male and female phases were equal in time (df = 1, F = 1.33, p = 0.261). Pollen was presented on the trichomes and was available to insects for 20–36 hours. After the pollen was released from anthers, the style elongated and the female phase was correlated with the unfolding of the stigma lobes. When the lobes unfolded, the style was 2–4 times longer than at the beginning of the male stage. The studied *Campanula* species had either stigmas positioned vertically (*C. persicifolia*, *C. trachelium*) or stigma lobes coiled up like a spiral and touched the style towards the end of the anthesis (*C. glomerata*). During the development of the flowers for all the studied species, the corolla changed the colour. The flower life-span differed between species and was the longest for *C. persicifolia* – *ca.* 5.5 days and lasted *ca.* 3.5 days in *C. glomarata* and *ca.* 3.0 days in add in before *C. trachelium*.

Nectar production

A ring-like nectar glands are concealed in the expanded bases of the stamens. No nectar was detected in bud stage (tab. 3). In the male phase, trace amount of nectar was detected in every *Campanula* species (fig. 2). For all the species, nectar accumulation was gradual during the flower life-span, and the highest accumulative nectar production and sugar mass were noted in the female-phase flowers. The amount of nectar sugars produced add the female phase reached 70–87% of the maximum nectar produced by a flower. The same pattern was observed in 2012 and 2013. The period of nectar production varied between species and lasted *ca.* 5.0 days (*C. persicifolia*), or 2.5–3.0 days (*C. trachelium* and *C. glomerata*). A single flower of the studied species produced relatively low amounts of nectar (extreme values: 0.6–12.4 mg/flower) of changeable concentration (extreme values: 33.0–62.0%). The total nectar sugars production per flower was found to differ significantly between study species (*F* = 7.828, df = 2, *P* = 0.044; tab. 4). The lowest amount of sugars was produced in the flowers of *C. persicifolia*; almost 30–40% more nectar sugars was produced in the flowers of *C. glomerata* and *C. trachelium*. Intra-species differences in the total amount of sugars produced per flower between two study years was found for each species (*F* = 5.341, df = 1, *P* = 0.012 – *C. persicifolia*; *F* = 3.87, df = 1, *P* = 0.027 – *C. glomerata*; *F* = 7.77, df = 1, *P* = 0.031 – *C. trachelium*). The amount of sugars produced per flower was 2–2.5 times higher in 2013 compared to 2012. The total sugar yield was 1.9 g/10 m^2 for the *C. persicifolia*, which was 2.5–3.5 times lower than established for *C. glomerata* or *C. trachelium*.

Table 3. Some aspects of nectar production process in the studied *Campanula* species

Phase	*C. persicifolia*	*C. glomerata*	*C. trachelium*
Amount of nectar in bud	not present	not present	not present
Nectar amount at the female stage of the maximum produced by the flower	87%	79%	70%
Secretion period (days)	5.0	3.0	2.5
Resorption period (days)	0.5	0.5	0.5

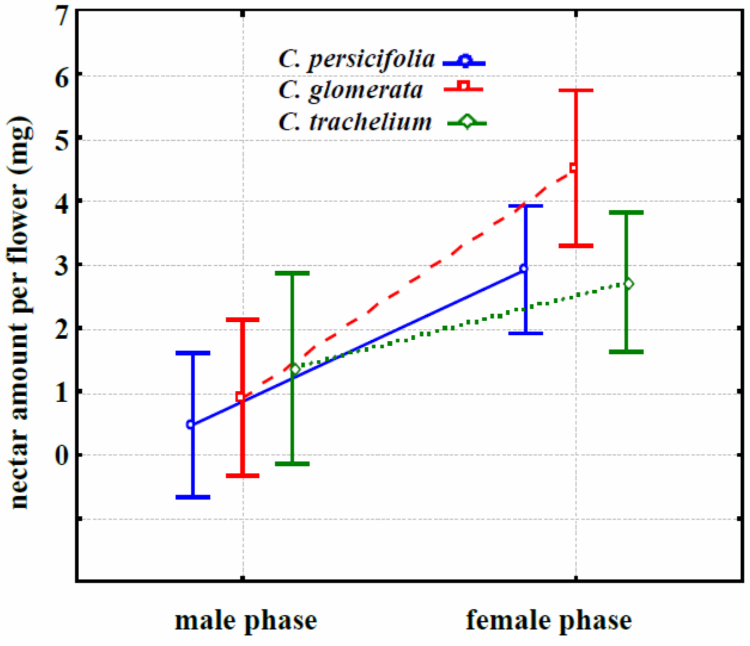

Fig. 2. Phase effect on nectar accumulation in three *Campanula* species. Values are means calculated across the years of study. Vertical bars show 95% confidence intervals

Table 4. Sugars concentration in nectar and amount of sugars produced by *Campanula* species studied in the years 2012–2013

Species	Year	Number of examined flowers	Concentration of sugars in nectar (%)			Total sugars yield	
						per flower (mg)	10 m^2 (g)
			mean	±SD	V (%)	mean	mean
C. persicifolia	2012	88	42.5_a	10.2	24.0	1.1_a	0.4
	2013	95	53.2_b	7.8	14.7	2.1_b	3.4
	Mean		47.9_B		18.8	1.6_A	1.9
C. glomerata	2012	78	45.0_b	6.6	14.7	1.3_a	1.0
	2013	45	35.1_a	10.3	29.3	3.4_b	12.2
	Mean		40.1_A		21.1	2.4_B	6.6
C. trachelium	2012	95	52.9_a	8.9	16.8	1.2_a	1.7
	2013	44	60.5_b	12.6	20.8	3.1_b	9.0
	Mean		56.7_C		19.0	2.2_B	5.4

Mean values ±SD are given. Means within columns with the same small letter do not differ significantly between years within a species and means with the same capital letter do not differ significantly between species based on Tukey's test at $\alpha = 0.05$

DISCUSSION

The flower life-span differed between *Campanula* species. The variance in flower life-span could be due to genetic or to environmental factors [Evanhoe and Galloway 2002, Denisow 2009]. Flowers of the studied *Campanula* species are protandrous. Sex change and earlier maturation of anthers than stigma receptivity have also been reported in other *Campanula* species [Evanhoe and Galloway 2002, Schlindwein et al. 2005]. The length of male and female phases differed between species, however the male phase was shorter than the female phase. Different duration of sexual phases in dichogamous flowers was reported by Bertin and Newman [1993], and different patterns were reported for *Campanula* species, e.g. in *Campanula rapunculus* the duration of both male- and female-phases was equal [Schlindwein et al. 2005], male-phase was shorter by approximately 50–90% compared to female-phase in nine *Campanula* species studied in Greece [Blionis and Vokou 2001]. The longevity of sexual phases is interpreted as an optimal strategy for flower cross-pollination and for reduction of the costs of flower maintenance [Gao et al. 2015]. However, as reported by Evanhoe and Galloway [2002], the sexual phases duration exhibit plasticity and longevity of the phases can by modified by pollen removal from pollen presenter (male phase shortening) or by pollen deposition on stigma (female phase shortening). Therefore, the flower life-span and expression of sexual phases may vary depending, e.g. on the frequency of pollinators or even their assemblage.

The studied *Campanula* flowers offer both nectar and pollen for insect visitors. Most of the flowers open between 10.00 and 16.00 h, similarly not synchronized opening time was described for the flowers of *C. rapunculus* by Schlindwein et al. [2005]. Similar pattern was also observed in *C. bononiensis* [Denisow et al. 2014] and in *C. patula* (personal observation; unpublished data).

In our study, the female phase flowers of *C. persicifolia*, *C. glomerata*, and *C. trachelium* produced 2–3-fold more nectar than the male phase. The gender-biased nectar production pattern has been revealed in diverse dichogamous flowers [Pacini and

Nepi 2007], however, the male-biased or female-biased nectar production have been documented in several protandrous species and is thought to be driven by sexual selection or avoidance of inbreeding [Carlson 2007]. In *Campanula* species, female-biased pattern of nectar secretion combined with a pattern of flower opening contribute to the formation of nectar production gradient along the inflorescences and can influence insect behaviour and impose insect movements between individuals. The female-biased nectar secretion in protandrous flowers can be also interpreted as compensatory mechanism to continue sex function in the flower with not pollen available and to enhance female reproductive success, as suggested by Inoue [1990] or Pei et al. [2011].

We have revealed the differences in nectar characteristics (sugar concentration, sugar amount) between the *Campanula* species. Plant species vary greatly in the rate at which their flowers produce nectar sugars [Pacini and Nepi 2007]. For example, Pacini et al. [2003] claim that the quantity of nectar sugars produced by a flower correspond to the volume of the cells of nectary parenchyma or nectary type (photosynthetic or non-photosynthetic). No precise microscopic observation were performed here and it is the recommendation for further studies.

As in many angiosperms, differences in nectar sugar concentration and sugar mass produced are mainly due to weather conditions (e.g. air humidity, air temperature) [Denisow 2005, Pacini and Nepi 2007]. It is because the photosynthetic activity of the plant and corolla parts are responsible for production of sugar constituents of nectar, although the storage organs might also contribute to nectar production. Nectar volume and sugar concentration can be also considered as adaptation to pollinator types that visit flowers and/or pollinate flowers [Galetto and Bernardello 2004, Pacini and Nepi 2007].

The total sugar yield (0.4–12.2 g/10 m^2) established for the studied *Campanula* species is low compared to other herbaceous meadow species. For example, *Salvia pratensis* can yield 116–217 g/10 m^2 of sugars [Jabłoński and Kołtowski 2001]. However, *Campanula* plants support insect visitors with high amount of pollen [Denisow and Wrzesień 2015]. In fact, we observed generalist insect species visiting flowers of the species studied here, e.g. *Apis mellifera*, *Bombus* spp., other Hymenoptera, Diptera, Coleoptera, Syrphidae, Lepidoptera. Our previous observations also revealed diverse pollinators groups attracted by *Campanula* flowers [Denisow and Wrzesień 2015]. According to various authors, in order to conserve insect pollinator biodiversity, the preservation and maintenance of diverse flowering plants is required [e.g. Fussell and Corbet 1992, Biesmeijer et al. 2006, Hicks et al. 2016].

CONCLUSIONS

1. The length of blooming differed between study species and years. *Campanula persicifolia* was the first to bloom (end of May/beginning of June), followed by *C. glomerata* and *C. trachelium*. All the species ended blooming in the second decade of August.
2. Flowers of studied species are protandrous with the female phase 1.5–3-fold longer than the male phase (*C. persicifolia* and *C. glomerata*) or with equal duration of the phases (*C. trachelium*).
3. Female-biased nectar production pattern was found in the *Campanula* species; 70–87% of nectar amount was produced in the female phase.
4. Mean nectar sugars concentration ranged from 40.1% (*C. glomerata*) to 56.7% (*C. trachelium*). The highest sugar-yielding species was *C. glomerata* with 2.4 mg of sugars per flower and 6.6 g of sugars per 10 m^2.
5. *Campanula* species are attractive as pollen and nectar producing plants and can be used as possible addition to support pollinators in home gardens or on idle lands.

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