

Original Article

EARLY SPRING NECTAR AND POLLEN AND INSECT VISITOR BEHAVIOR IN TWO *CORYDALIS* SPECIES (PAPAVERACEAE)

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Abstract

This study, conducted in 2008 and 2012 - 2013, evaluated the flowering pattern (seasonal and diurnal), the abundance of flowering, nectar, and pollen yield, and insect visitor activity for *Corydalis solida* (L.) Clairv. and *C. cava* Schweig. et Koerte. The populations occur in the ground layer of a deciduous forest (Fagetalia ordo, Querco-Fagetea class) in a natural gorge within the current area of the UMCS Botanical Garden in Lublin, Poland (51° 16' N, 22° 30' E). The phenology of *Corydalis* species showed distinct year-to-year plasticity (e.g., blooming period in March - April or in April - May; duration 18 - 42 days). The most intensive flower opening was noted in the early morning hours (85 - 90% of daily openings occurred between 6.00 and 10.00 h, GMT +2 h). The average sugar yield was similar at 4.6 kg/ha (*C. cava*) and 5.2 kg/ha (*C. solida*), but the average pollen production differed and reached 2.1 kg/ha (*C. cava*) and 4.1 kg/ha (*C. solida*). The flower-visitor interaction in *Corydalis* species involved both biological (early pattern of diurnal flowering, protandry, pollen presentation at the moment of anthesis) and morphological (nectar hidden in deep spur) features. *Apis mellifera* foragers predominated on both *Corydalis* species (mean of total visitors, 68.0% to *C. solida*; 62.5% to *C. cava*) and foraged mainly for pollen (82% of foragers), while bumblebee queens (mean of total visitors, 32.0% to *C. solida*; 37.5% to *C. cava*) collected mainly nectar (68.0% of foragers).

Keywords: *Apis mellifera*, bee pasture conservation, *Bombus* spp., deciduous forests, floral rewards.

INTRODUCTION

Open and forest/scrub habitats are documented as familiar for bees (Apoidea) (Banaszak, 1983; 1992). In Poland, total forest area is 9.1 million ha (ca. 28.0% of acreage) (Wasiak, 2013). Habitats of deciduous forests constitute 45.5% of the total forest area and are critical in the maintenance of the food continuity supply for visiting insects and potential pollinators of commercial crops (Delaplane and Mayer, 2000; Kołtowski, 2006; Lipiński, 2010). The melliferous value has been established for several forest species in the former Soviet Union by Gluchov (1950), in Ukraine by Bodnarczuk et al. (1993), and in Poland by Szklanowska (1973; 1979). Palynological research confirms that forest vegetation makes

up a large proportion in the Apoidea diet, mainly in spring (up to 40%) (Teper, 2006; Stawiarz and Wróblewska, 2010). The flower-visitor interaction is based on various relationships, including physiological and biological interactions (Faegri and van der Pijl, 1979; Fahn, 1988; Ashman and Shoen, 1994; Goulson, 1999). Understanding these interactions is essential during the selection of plants for effective bee pastures (Delaplane and Mayer, 2000).

The species of the genus *Corydalis* are temperate zone geophytes that are native to northern Europe and Asia, and they prefer open moist meadows or shady forest habitats (Higashi et al., 1988; Bodnarczuk et al., 1993; Olesen, 1996; Goldenberg and Zobel, 1997; Yasaka et al., 1998; Zhang et al., 2009). In Poland, the *Corydalis* species develop on

deciduous forest types of habitat characteristic for phytocoenoses from Fagetalia ordo, Querco-Fagetea class (Matuszkiewicz, 2012). The species from the genus *Corydalis* are also frequent on stream and river banks, at the bottom of precipices, and in parks (Rutkowski, 2004).

This paper describes one in a series of studies on the nectariferous and polleniferous potential of species across natural plant communities (e.g., Denisow, 2009a, 2011). The main issue here was to determine the relationship between blooming biology (phenology, diurnal pattern, flower morphology, floral reward) and the insect visitors for *Corydalis solida* and *C. cava*. We also estimated the total nectar and pollen yield to evaluate if *Corydalis* species are suitable for enriching early spring bee pastures.

MATERIAL AND METHODS

Study site

Observations were conducted in the years 2008 and 2012 - 2013. The experimental patches, with the vegetation typical for the ground layer of deciduous forest (Querco-Fagetea class), were located in a natural gorge within a current area of the Botanical Garden of Maria Curie-Skłodowska University, in Lublin, Poland (51° 16' N, 22° 30' E, 200 m a.s.l.). The tree layer consisted of *Acer platanoides* L., *Tilia cordata* Mill., *Fagus sylvatica* L., and *Padus avium* Mill., and in the shrub layer, *Sambucus nigra* L. and *Corylus avellana* L. occurred.

Study species

Corydalis solida (L.) Clairv., and *C. cava* Schweig. et Koerte belong to the family Fumariaceae (Rutkowski, 2004) or Papaveraceae according to the modern APG III system (Angiosperm Phylogeny Group, 2009). The plants are perennials with the bulb developing at a depth of 5 - 10 cm. Flowers, arranged in a raceme inflorescence, are perfect, zygomorphic and consist of two sepals and two pairs of converging petals; one of the outer pair is formed into a short and rounded bag-like spur, and the inner petals are connected at the tip (Heywood, 1985; Rutkowski, 2004).

Flowering and insect visitor activity

Protocols described by Jabłoński and Szklanowska (1997) and Denisow (2009b) were applied. During the growing seasons, the onset and length of the blooming period was established. Because of the time investment required for the observations, the diurnal pattern of blooming was established

only in 2008 and 2013. The observations were conducted from 6.00 until 19.00 (GMT + 2.00 h), and in one-hour intervals, newly opened flowers were counted ($n = 15$ inflorescences per species). Simultaneously, the pattern and intensity of insect visits were recorded ($n = 4$ random plots, 1 m², per species). These observations were conducted for three consecutive days, at the full bloom phase of the population. During each census of observation (3 - 6 min), the total number of visiting insects was recorded and the type of forage (nectar vs. pollen) noted. To determine the flower lifespan, the buds ($n = 8 - 12$ per year) were randomly chosen and marked on different individual plants. The entire flower lifespan was defined as the period from bud opening until petal wilting. The number of florets per raceme ($n = 24 - 30$) and the number of inflorescences on random circular areas 0.1 m² (36.7 cm in diameter) were established. The data were converted to the number of flowers per 1 m² of the surface and used to estimate the total nectar and pollen yield.

Nectar secretion

We examined secretion using the tulle isolators and the pipette method (Jabłoński, 2002). The data from 2008 and 2013 are presented, as some isolators in 2012 were stolen, and the remaining samples seemed to be unrepresentative. Nectar collection was conducted in 3 - 5 replications during the blooming period. In each replication, 5 - 7 samples were collected; a single sample contained nectar from 11 - 20 flowers. Total sugar concentration was measured with an Abbe refractometer. Nectar volume and sugar concentration were used to calculate the total sugar mass in each sample. Relevant calculations allowed determination of the amount of sugars produced per 10 flowers (in mg) and per unit area (in kg).

Pollen production

The mass of pollen was determined in the full blooming phase. Mature but unopened anthers ($n = 200$) were collected in weighed glass containers in four replications. Subsequently, 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 and with 70% ethanol. Pollen viability was tested in standard acetocarmine slides ($n = 300$).

Meteorological factors

Weather data were obtained from a local weather station. Monthly and decade means were compared to the long-term data (1951 - 2010). The year 2008 was colder compared to the long-term data, with the exception of the initial months of the year (January, February, and March), when the air temperature was on average above (0.4 - 1.8°C) the long-term data (mean = -3.8°C). The total precipitation in February was 70% lower than long-term data (mean = 40.2 mm). February 2012 was relatively cold (5.4°C lower compared to the long-term mean); conversely in March and April, 1.2°C and 3.8°C above the norm was recorded, respectively. The precipitation level of the autumn-winter of 2012 - 2013 was approx. 70% lower than in the long term. The first months of the year 2013 were colder compared to the long-term data, with an extremely high snow layer noted in April.

Data analysis

Data are presented as means with SD. The standard analysis of variance was applied (Stanisz, 1996). Post hoc comparison of means was done using the Duncan t-test. The level of statistical significance for all analyses was set at $\alpha = 0.05$. All analyses were performed using Statistica ver. 6.0 (StatSoft Poland, Krakow).

RESULTS

Corydalis species were among the earliest blooming species in the studied patches and co-flowered with *Galanthus nivalis* L. and *Hepatica nobilis* Mill. The termination of *Corydalis* species blooming overlapped with the full blooming of *Anemone nemorosa* L. and with the initial phase of blooming for *Pulmonaria obscura* L. Under the climatic conditions of eastern Poland, during the study seasons, the blooming of *Corydalis* species occurred in March-April or in April-May (Tab. 1). The length of the flowering period differed between species and between growing seasons. In each study year, *C. solida* started to bloom first (approx. a week earlier than *C. cava*). The length of the flowering period ranged from 19 to 42 days for *C. solida* (mean = 30.0 ± 11.5) and was one week longer than the flowering length of *C. cava* (range 18 - 37 days; mean = 28.3 ± 9.6). The seasonal rhythm of flowering in 2008 differed significantly from that in 2013 (Fig. 1). In the first two weeks of 2008, the flower development rate was slow (up to 5% per day), and the peak of flowering for the population was observed in the third week, in contrast to 2013 when the flowering peak had already occurred on the fifth day of the flowering period, with more than 60% of the total flowers opened in the first week.

Table 1.

Time and length of flowering and flower lifespan for *Corydalis solida* and *C. cava* in 2008 and 2012 - 2013, observed in SE Poland (mean \pm SD)

Species	Year	Flowering		Number of flowers per inflorescence		Number of inflorescences per 1 m ²		Number of flowers per 1 m ²		Lifespan per single flower (d)	
		Date	Length (d)	Mean	\pm SD	Mean	\pm SD	Mean	\pm SD	Mean	\pm SD
<i>C. solida</i>	2008	29.02 - 10.04	42	11.6 _a	3.2	33.0 _a	20.3	385.0 _a	295.0	14.2 _c	5.2
	2012	20.03 - 17.04	29	14.7 _b	5.2	70.0 _b	58.2	1050.8 _b	1148.3	11.5 _b	7.3
	2013	12.04 - 1.05	19	15.9 _b	4.4	73.7 _b	43.6	1122.7 _b	688.9	6.6 _a	3.1
	Mean		30.0	14.1 _b	4.6	58.9 _A	44.6	852.6 _B	77.8	10.8 _A	8.2
<i>C. cava</i>	2008	10.03 - 15.04	37	10.4 _b	3.4	96.5 _c	31.7	941.5 _c	287.8	10.3 _b	2.4
	2012	26.03 - 24.04	30	7.6 _a	2.5	57.5 _b	15.4	444.2 _b	203.0	7.1 _{ab}	3.2
	2013	18.04 - 5.05	18	9.4 _b	2.7	26.0 _a	13.8	246.7 _a	166.8	5.1 _a	2.1
	Mean		28.3	9.1 _A	3.0	60.0 _A	37.8	544.1 _A	377.4	7.4 _A	2.8

Means in columns with the same letters are not significantly different at $\alpha = 0.05$ (Duncan t-test).

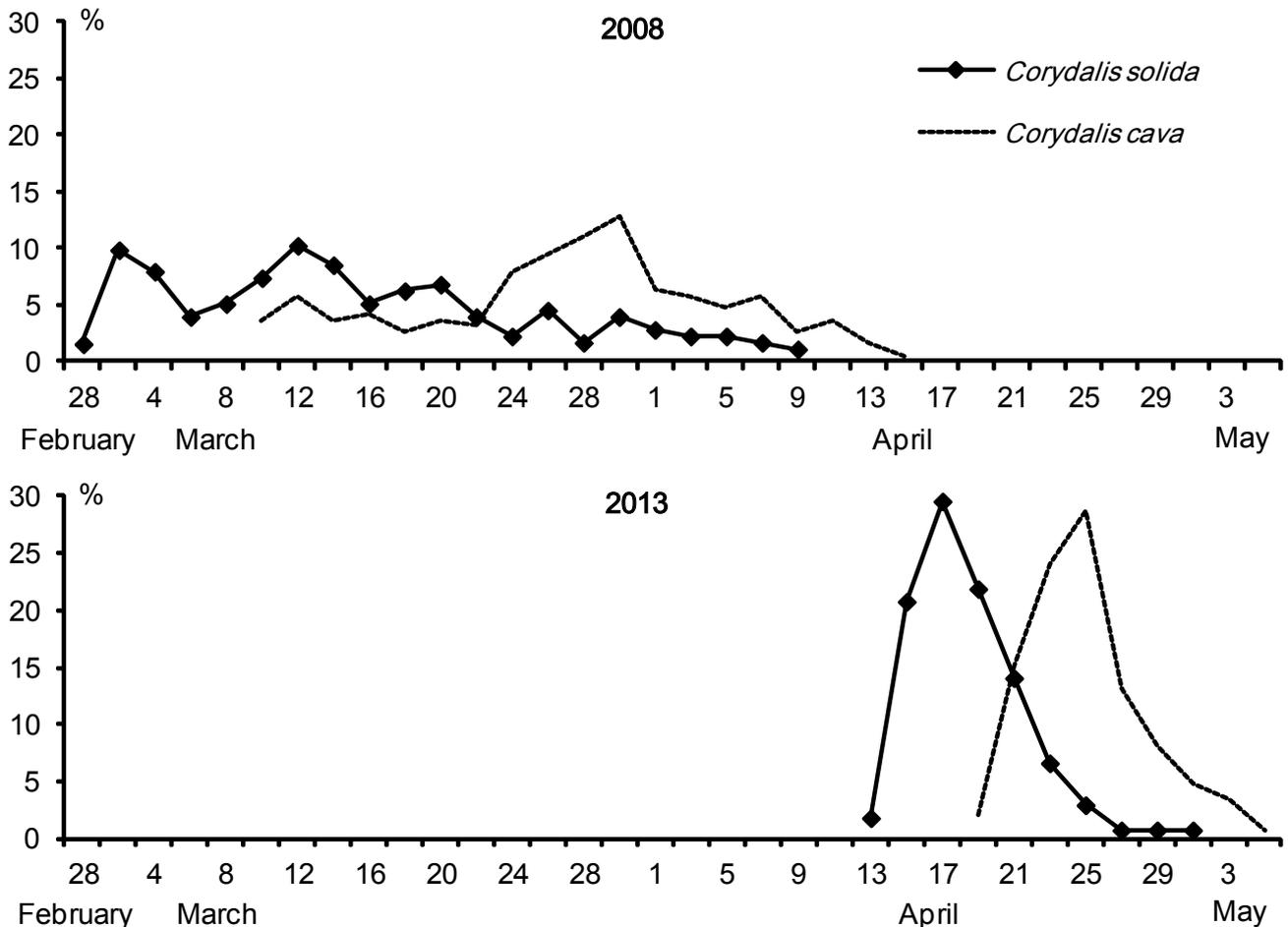


Fig. 1. Seasonal rhythm of blooming of *Corydalis solida* and *C. cava* in 2008 and 2013, expressed as a percentage of flowers blooming in consecutive days of flowering in relation to the total number of flowers developed during the flowering season, observed in SE Poland.

Flowers of both *Corydalis* species aggregate in racemes and commence blooming acropetally, with an early diurnal flower opening pattern (Fig. 2). About 30 - 40% of the daily openings were observed at 6.00 h (GMT+2 h), followed by a rapid progression, and up to 85 - 90% of flowers opened before 10.00 h, until termination was recorded at about midday.

The inflorescence size ($F_{1,122} = 49.61$, $p = 0.004$) and flower density ($F_{1,122} = 10.84$, $p = 0.001$) differed significantly between the study species (Tab. 1). The single raceme of *C. solida* developed more flowers (mean = 14.1 ± 4.6 , range 8 - 24) than the raceme of *C. cava* (mean = 9.1 ± 3.0 , range 6 - 16). Significant year-to-year differences were noted in the number of flowers per inflorescence ($F_{2,59} = 6.59$, $p = 0.002$, *C. solida*; $F_{2,59} = 3.34$, $p = 0.041$, *C. cava*) and in the number of flowers per 1 m^2 ($F_{2,59} = 6.9$, $p = 0.002$, *C. solida*; $F_{2,59} = 60.9$, $p < 0.001$, *C. cava*). The intraspecific disparities in the abundance of blooming between years were

3 - 4 fold. No species effect was found for the duration of the flower lifespan ($F_{1,72} = 37.61$, $p = 0.104$), but significant year-to-year differences were noted for the duration of anthesis within both species studied ($F_{2,59} = 14.21$, $p = 0.021$, *C. solida*; $F_{2,59} = 26.8$, $p = 0.017$, *C. cava*). In the years 2008 and 2012, the single flower lifespan was 4 - 8 days longer for *C. solida*, and 2 - 3 days longer for *C. cava* as compared to 2013.

In the flowers of both *Corydalis* species, the nectary glands form the protuberance located above the pedicel, and the bag-like spur serves as a reservoir for nectar (Fig. 3C). The spur is formed from the outer part of two converging petals. The amount of secreted nectar ($F_{1,36} = 24.05$, $p < 0.001$) and the concentration of sugars ($F_{1,36} = 86.62$, $p < 0.001$) varied significantly between species. The flowers of *C. solida* secreted 2-fold higher amounts of nectar (mean = 26.6 ± 7.5 mg per 10 flowers vs. 12.5 ± 8.6 mg for *C. cava*), with a lower sugar concentration (mean = 33.0 ± 14.2 vs. 54.0 ± 10.1 for

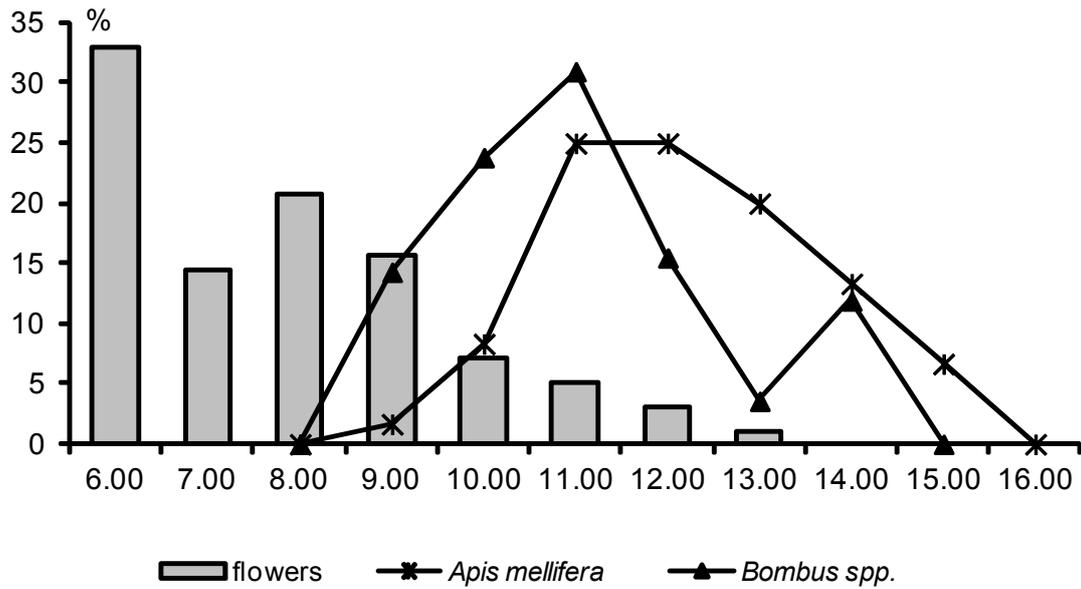


Fig. 2. Diurnal pattern of flowering expressed as the number of flowers opened at 1-h intervals in relation to the total opened during the day, and the diurnal activity of insect visitors observed in SE Poland (means calculated from *Corydalis solida* and *C. cava* and from 2008 and 2013).

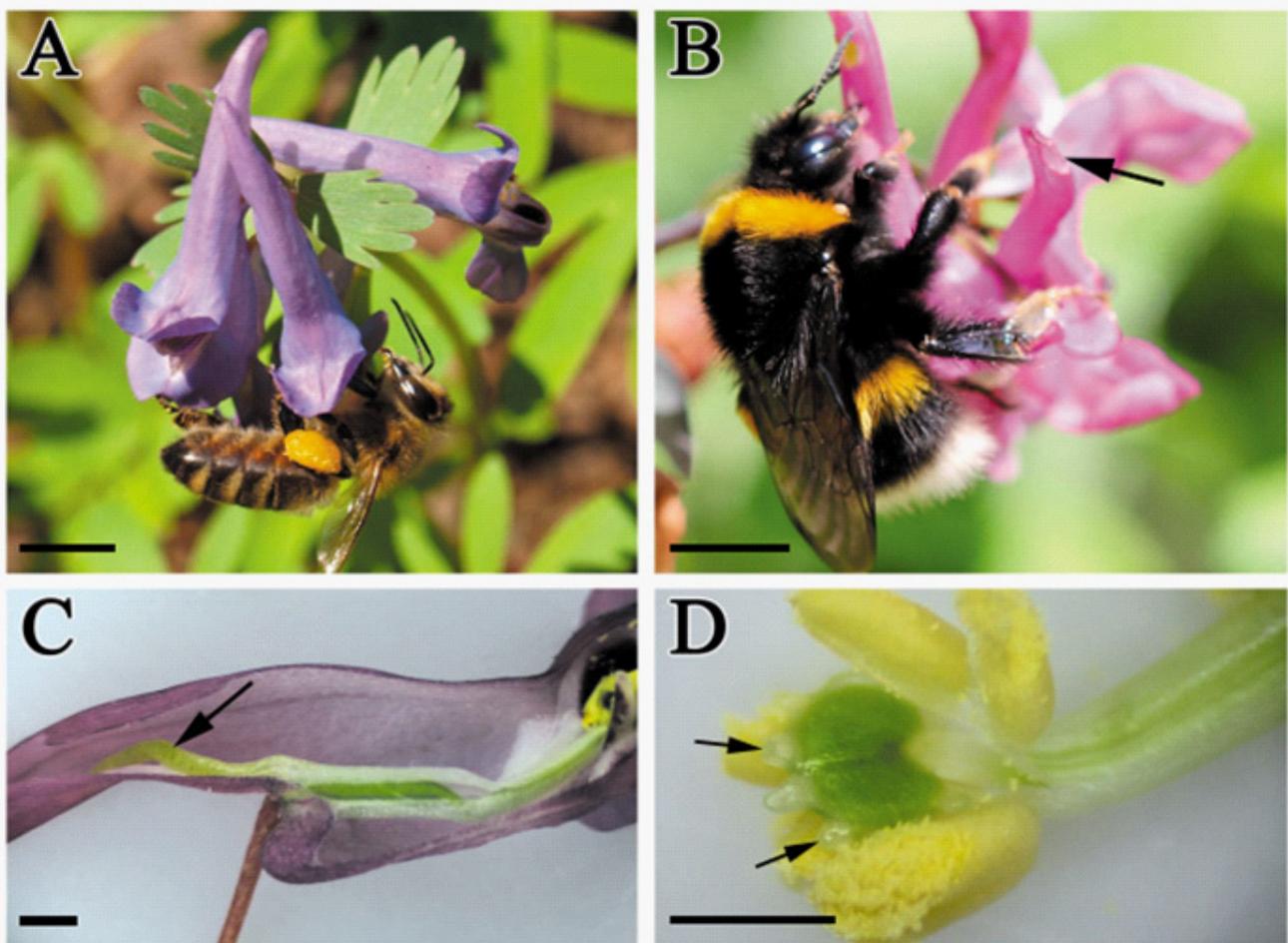


Fig. 3. Macro photographs of *Corydalis solida*. A. *Apis mellifera* with pollen loads (scale bar = 5 mm). B. *Bombus terrestris* during nectar robbery; note perforated spur (arrow) (scale bar = 5 mm). C. Longitudinal section through the flower with filiform nectary (arrow) located in the spur (scale bar = 1 mm). D. Bursting anthers at bud stage; note stigma with wings (arrows) (scale bar = 1 mm).

Table 2.

Concentration of nectar and amount of sugar delivered by <i>Corydalis solida</i> and <i>C. cava</i> in 2008 and 2013, observed in SE Poland (mean ± SD)									
Species	Year	Number of examined flowers	Concentration of sugars in nectar (%)			Sugars per 10 flowers (mg)			Total sugars yield (kg/ha)
			min - max	Mean	± SD	min - max	Mean	± SD	
<i>C. solida</i>	2008	102	19 - 31	27.3 _a	3.6	7.8 - 11.8	10.4 _b	7.1	4.0
	2013	123	36 - 47	38.6 _b	4.6	4.2 - 8.3	5.7 _a	1.4	6.4
	Mean			33.0 _A	14.2		8.1 _A	10.1	5.2
<i>C. cava</i>	2008	114	50 - 60	49.2 _a	5.2	9.0 - 15.0	8.5 _b	3.5	8.0
	2013	131	51 - 68	58.7 _b	3.8	1.1 - 8.0	4.7 _a	2.0	1.2
	Mean			54.0 _B	10.1		6.6 _A	5.6	4.6

Means in columns with the same letters are not significantly different at $\alpha = 0.05$ (Duncan t-test).

Table 3.

Dry mass of anthers, mass of produced pollen, total pollen yield, and pollen viability in two <i>Corydalis</i> species in 2008 and 2012 - 2013, observed in SE Poland (mean ± SD)										
Species	Year	Mass of dry 100 anthers with pollen (mg)			Mass of pollen per 100 anthers (mg)			Total pollen yield (kg/ha)	Viability (%)	
		min - max	Mean	± SD	min - max	Mean	± SD		Mean	± SD
<i>C. solida</i>	2008	4.1 - 5.9	4.9 _a	0.8	1.6 - 3.5	2.2 _a	0.9	1.5	74.2 _a	2.2
	2012	6.7 - 8.6	7.5 _b	0.9	2.7 - 4.1	3.3 _b	0.6	6.3	82.1 _b	4.1
	2013	3.8 - 6.5	5.0 _a	1.2	2.3 - 3.3	2.9 _a	0.5	4.5	89.3 _c	3.9
	Mean		5.8 _A	1.5		2.8 _B	0.7	4.1	81.9 _A	7.2
<i>C. cava</i>	2008	2.7 - 4.7	3.6 _a	0.9	0.8 - 1.2	1.0 _a	0.2	2.6	87.2 _a	3.1
	2012	3.5 - 5.1	4.3 _a	0.9	1.6 - 2.2	1.9 _a	0.3	1.5	94.4 _b	1.8
	2013	9.3 - 13.1	10.8 _b	1.7	1.0 - 2.1	1.6 _a	0.5	2.1	99.8 _c	0.2
	Mean		6.2 _A	3.6		1.5 _A	0.5	2.1	93.8 _B	8.1

Means in columns with the same letters are not significantly different at $\alpha = 0.05$ (Duncan t-test).

C. cava) (Tab. 2). No species effect was found for the total sugar mass produced in flowers ($F_{1,36} = 2.90$, $p = 0.097$). The studied nectar characteristics varied among growing seasons (amount of nectar, $F_{1,36} = 28.60$, $p < 0.001$; sugar concentration, $F_{1,36} = 9.04$, $p = 0.004$; sugar mass, $F_{1,36} = 30.64$, $p < 0.001$). The mass of produced sugars in 2008 was almost twice that of 2013. The average sugar yield of the two *Corydalis* species was similar 4.6 kg/ha

(*C. cava*) and 5.2 kg/ha (*C. solida*). Considerable differences were noted between years, however, mainly in the case of *C. cava* (1.2 - 8.0 kg/ha). In the flowers of the *Corydalis* species, filaments of the stamens are fused in two sets. Each group consists of one complete (2 anthers) and two incomplete stamens (1 anther), which results in 8 anthers per flower (Fig. 3D). The pollen is released in the bud stage and is shed into the cavity of

the wing-plates that cover the top of the stigma. Generally, the anthers of both species were similar in size ($F_{1,21} = 0.28, p = 0.602$) but delivered significantly different amounts of pollen ($F_{1,21} = 23.72, p < 0.001$). The anthers of *C. solida* produced twice as much pollen as *C. cava*, on average 2.8 mg and 1.5 mg per 100 anthers, respectively (Tab. 3). This species effect also was found for pollen viability ($F_{1,33} = 43.12, p = 0.032$), with more viable pollen grains observed in *C. cava*. The average estimated pollen productivity per unit area depended on the species and related to the abundance of blooming and changeable mass of pollen produced in anthers. In the full flowering phase, the pollen yield was 2.1 kg/ha (*C. cava*) and 4.1 kg/ha (*C. solida*).

Corydalis solida and *C. cava* received visits from *Apis mellifera* and female bumblebees (*Bombus* spp.) (Fig. 3 AB). In the early morning hours, bumblebees dominated, representing about 80% of the visits between 9.00 - 10.00 h; between 11.00 - 15.00 h, honeybees predominated (Fig. 2). The insect visitors initiated visits at about 8.00 - 9.00 h and finished activity at 15 - 16.00 h, about the same time every day, irrespective of species.

The insect visitor response to the air temperature was observed. When the maximum daily air temperature was under 12°C, honeybees did not visit the *Corydalis* flowers at all whereas bumblebees visited the *Corydalis* flowers very rarely. *Apis mellifera* predominated on both *Corydalis* species (mean of total visitors, 68.0% for *C. solida* and 62.5% for *C. cava*)

and constituted 65.3% of visitors, on average (Fig. 4A). The honeybees foraged mainly for pollen while bumblebees collected mainly nectar, irrespective of plant species (Fig. 4B).

DISCUSSION

The flowering of *C. solida* and *C. cava* took place before the trees of the canopy layer began developing leaves, which is typical for the spring ground layer flora of deciduous forests (Gluchov, 1950; Szklanowska, 1979; Lipiński, 2010). The study period included years with a great contrast between the warm spring of 2008 and cold spring of 2013, in which locally over 27 cm of snow layer during the month of April was noted. Thus, the disparity between 2008 and 2013 for the onset of blooming for *Corydalis* spp. was 30 days. The influence of meteorological factors, i.e., air temperature and precipitation level, on the onset, duration, and abundance of flowering has been described for different taxa (Jabłoński and Szklanowska, 1997; Denisow, 2009a, b). In natural communities, the differences for the onset and duration of the blooming period were found for woodland herbs by Szklanowska (1979) and for ruderal species by Denisow (2011), and the disparities were particularly noticeable for the early spring taxa.

The flowering period of the two *Corydalis* spp. varied significantly, from 18 to 42 days. A similar duration of flowering (17 - 31 days) has been described for



Fig. 4. Participation of insect visitors in two *Corydalis* species observed in SE Poland. A. Means calculated from 2008 and 2012–2013 and proportion of nectar and pollen foragers of *Apis mellifera* and *Bombus* spp. B. Means calculated from *C. solida* and *C. cava* and from the years of study

Corydalis ambigua from an Asian temperate zone (Yasaka et al., 1998). Regardless of the species, we also identified differences in the seasonal flowering pattern. A long and slow distributed pattern was observed in the year 2008, with air temperature on average stable during flowering, or slightly below the norm, while the pattern in 2013 shifted to shorter and explosive with considerably delayed flowering in the season. Generally, plants differ greatly with respect to the manner of flower display in the season, depending on flowering time or environmental conditions (Jabłoński and Szklanowska, 1997; Denisow, 2009b). Seasonal development of flowers from continuous to asymmetrical has been observed for different taxa, e.g., *Geranium platypetalum* (Masierowska, 2012). In natural plant communities, flowering expanded in time is especially characteristic for the species that bloom at the beginning of the growing season (Denisow, 2011) and is considered as a part of both the pollination system and reproductive strategy (Faegri and van der Pijl, 1979). As emphasized by Goulson (1999), the insect populations are small in size during the initial weeks of the growing season, and the character of seasonal *Corydalis* species blooming seems to be adapted to low insect visitor density. Synchronous blooming of the flowers of the species in a given plant population is very important for the energetics of pollination. Early in the season, temperature drops are frequent; therefore, the pattern of blooming minimizes the energy expenditure of the pollinators flying between plants (Heinrich and Raven, 1972; Kudo and Ida, 2013).

The corolla of the studied *Corydalis* species persisted on the pedicel even for 14 days, which is consistent with the findings of Olesen (1996) for *C. solida* in Danish forests (approx. 9 - 14, up to 25 days of flower longevity). The flower lifespan depends in part on the air temperature, air humidity, and whether or not the flower is pollinated (Ashman and Shoen, 1994; Denisow, 2009a). Prolonged anthesis is important, especially in the case of the early spring blooming species, and may raise the probability that flowers are visited by pollinators. The flower lifespan may also change depending on the phenology. Yasaka et al. (1998) documented a shorter anthesis of *C. ambigua* flowers blooming in the late season compared to blooming in the earlier season. Accordingly, in our study, shorter anthesis was recorded in 2013, in the late flowering time (April–May), as compared to the early flowering time (March–April) in 2008.

The studied species developed numerous flowers per inflorescence; however, the racemes of *C. solida* developed more flowers, which confirms the descriptions of Rutkowski (2004) and indicates that this feature is highly genetically determined. The density of flowers per 1 m² varied substantially among growing seasons (247 - 1122). The considerably lower abundance of blooming-only 165 flowers per m² for *C. solida* was noted by Szklanowska (1979). As highlighted by different authors, the habitat (soil type, nutrients) and environmental conditions (temperature, humidity) are essential for the abundance of blooming (Lipiński, 2010; Denisow, 2011). Also, the dynamics of the population, i.e., the participation of generative and vegetative individuals, is changeable during the life history of clonal species, which may considerably affect the abundance of blooming (Goldenberg and Zobel, 1997). Although a detailed population study was not planned, we observed a changeable proportion of generative and vegetative individuals in the patches during the years of study. Additionally, in a woodland community, the progress of herbaceous species is limited by interspecies competition from, for example, shrubs and trees. Numerous juvenile and adult individuals of shrubs and trees were found, overgrowing in the bottom of the loess gorge where the population of *C. cava* occurred. An increase in the density of canopy closure results in an unsuitable habitat for photosynthesis and limits the portion of the starch stored in the underground vegetative organs and thus carbohydrates allocated to reproductive organs; the consequence can be reduced abundance of flowering. Goldenberg and Zobel (1997) reported poor growth and a decrease in the flowering for *Corydalis aquae-gelidae*, also a forest species, when the canopy level reached over 90% closure.

The strategies for luring insect visitors to *Corydalis* flowers involve various features. Because of the early phenology, the *Corydalis* species are attractive to *A. mellifera* and bumblebee queens. The character of floral reward and the morphological and biological flower traits affect the behavior of insect visitors. We observed nectar-robbing behavior of bumblebees, which is similar to bumblebee foraging behavior on *Corydalis* described by Higashi et al. (1988). Nectar robbing occurs in over 150 flowering species across 40 botanical families and relates to flower type (floral tubes or nectar spurs) with deeply hidden nectar (Faegri and van der Pijl, 1979). Nectar in the studied *Corydalis* species was accumulated in the deep spur and was difficult to obtain by short-tongued bees; thus, honeybees frequently avoided

it. At the same time, the highly protandrous flowers, with pollen release in the bud stage and pollen accessibility in the moment of flower opening, explain the preferences of *A. mellifera* in foraging mainly for pollen.

The total sugar yield (4.6 - 5.2 kg/ha) of the studied *Corydalis* species was much lower than established for other forest species, e.g., *Pulmonaria officinalis* L. (30 kg/ha) or *Ajuga reptans* L. (120 kg/ha) (Szklanowska, 1973; Kołtowski, 2006). However, the plants support insect visitors as one of the earliest energy food supplies during the growing season. According to various authors (e.g., Banaszak, 1992; Corbet, 2000; Delaplane and Mayer, 2000; Denisow, 2011), the conservation of all flower-visiting species within plant communities is required to maintain insect biodiversity. A shortage of food early in the season because of changes in the local flora may pose a serious threat to populations of pollinators, and an early blooming species (e.g., *Fritillaria meleagris*) might be a major food source for several species of bumblebees (Zych and Stpicyńska, 2011).

Our study is the first on the pollen yield of *Corydalis* species. The mass of pollen offered by *C. solida* anthers was 1.2 - 2.0 fold higher than that delivered by *C. cava*. As reported by Denisow (2009a, 2011), the mass of pollen produced is a highly genetically dependent feature and thus varies greatly among species, even within the same genera. Interestingly, regardless of taxon, we found no significant year-to-year differences in the mass of pollen produced in anthers. This result indicates that microsporogenesis and pollen production in these *Corydalis* species are resistant to external factors (e.g., temperature drops or precipitation shortage). This inference highlights the importance of *C. cava* and *C. solida* as a protein food for entomofauna, although differences in the total pollen yield between years were substantial (1.3 - 6.4 kg/ha). The fluctuation was mainly the result of the varied density of flowers, but an advantageous feature is annual spontaneous plant renewal, which ensures repeatable flowering.

In conclusion, *C. solida* and *C. cava* exhibit high phenotypic plasticity of timing of flowering and develop flowers with floral reward beneficial for Apidae visitors at the beginning of a growing season, a period of high food demand because of development of insect offspring. Increased planting of *C. solida* and *C. cava* as ornamentals in naturalistic parks and gardens may enrich poor early spring flowers, mainly in pollen for honeybees and carbohydrates for bumblebee queens.

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