FLORAL PHENOLOGY, FLORAL REWARDS AND INSECT VISITATION IN AN ORNAMENTAL SPECIES

Geranium platypetalum Fisch. & C. A. Mey., GERANIACEAE

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Received: 03.01.2012

Abstract

This 4-year study examined the flowering pattern, floral display, nectar and pollen production as well as insect visitation to a perennial Geranium platypetalum Fisch. & C. A. Mey. G. platypetalum bloomed from the end of May until the end of June. The pattern of flowering shows the skewed distribution with a tendency towards a more symmetrical curve. The flower display size fluctuated during the flowering season. The most intense blooming fell in the 2nd and 3rd flowering week. The flowers exhibit incomplete protandry.

Nectar productivity differed significantly between and stage of flower development. Ten and flowers secreted 29.8 mg and 17.6 mg of nectar, on average, respectively, with mean sugar content of 33.9% and 43.1%. The mean total sugar mass in nectar was similar for both stages and the values were 10.2 mg and 8.2 mg, respectively. Pollen mass per 10 flowers was 19.06 mg.

Bees (Apoidea) were the principal visitors on Geranium flowers. The peak of daily activity of visitors occurred between 10.00 and 14.00 hrs. The insects gathered mainly nectar. The mean visiting rate was 0.149 visit per flower×min⁻¹.

Increased use of G. platypetalum in parks and gardens is recommended in order to enrich the nectar pasture for A. mellifera and wild Apoidea.

Key words: Geranium platypetalum, flowering pattern, nectar, pollen, protandry, bees

INTRODUCTION

Variations in flowering phenology represent adaptation to various modes of pollination and are associated with the reproductive systems (reviewed in Goodwillie et al. 2010). Changes in flowering time allow plants to synchronize reproduction with conspecifics and pollinators, and to reduce competition for pollination (Waser and Real, 1979; Devaux and Lande, 2009). A quantitative characterization of flowering phenology is possible by examining the flowering distribution curve, i.e. the number of open flowers per census day for the whole flowering duration (Rathcke and Lacey, 1985). In plants that display multiple flowers simultaneously, the floral display, rather than the individual flower, is the basic unit of plant mating. Plants with large floral displays usually attract more pollinators than those that have small displays, and pollinators tend to visit more flowers on large displays (reviewed by Ohashi and Yahara, 2001; Kudo and Harder, 2005).

The flowering pattern of a species is of a great importance when the insect-plant relationships are investigated, especially if the taxon is considered as a food source for visitors. The Geranium species are among plants which can supply insects with ample nectar and pollen food.

The genus Geranium L. (Geraniaceae), crane’s bill, comprises approximately 400 species distributed in temperate areas and tropical mountains throughout most of the world (Zomflet, 1994; Aedo et al. 2007). According to Rutkowski (1998) 21 Geranium species occur in Polish flora. Some species are used as medicinal plants with antioxidant properties due to a high flavonoid and tannin content (Mikowska et al. 1998; Ghimire et al. 2006; Antal, 2010). They also provide essential oils (mainly geranium oil) for cosmetic purposes. Numerous crane’s bill species and cultivars are widely grown as ornamentals, especially in naturalistic parks and gardens. Their decorative value derives from beautiful and abundant flowers as well as from dense leaf canopies covering the ground. These plants are very easy in cultivation and perform well both in full sun and in shade conditions.
Geranium flowers appear to be typically entomophilous because of their visually attractive petals, robust stigmas, abundant pollen and the presence of active nectaries. Moreover, these actinomorphic flowers produce conspicuous nectar guides, generally similar on all petals (Link, 1990). Wild crane’s bills are eagerly visited by insects attracted mainly by nectar with a high sugar content.

Among taxa occurring in natural habitats, the best known, valuable nectariferous plants are Geranium pratense L. (Larsson and Shuel, 1982; Jabłoński, 1998; Lipiński, 2010) and G. sylvaticum L. (Jabłoński and Kotlinowski, 2002). Also, G. collinum Steph. (Mińkov, 1974), G. pheum L. (Mountain et al. 1981) and G. sanguineum L. (Masierowska, 2006) are listed among good melliferous species. Moreover, the presence of Geranium pollen was stated in pollen loads of honey bees (Hodges, 1952; Szwon and Martinovs, 1954) and bumblebees (Teper, 2002). Hymenoptera are the main insect visitors on flowers of different Geranium species (Proctor et al. 1996; Kandoori, 2002; Kozuharova, 2002; Masierowska, 2006).

In the recent literature there are very scarce data on plant-insect relationships in cultivated crane’s bills (Jabłoński and Kotlinowski, 2002; Masierowska, 2006). Ornamental species and cultivars planted in urban regions may help sustain local pollinator populations as well as broaden food source for maintained insects such as honey bees or some species of solitary bees and bumblebees (Denisow, 2008). These natural pollinators are of potential value in open and closed crop production systems and their population size should be increased by, among others, ensuring their refuges and nesting places as well as fulfilling food resource requirements (Goulson, 2003; Klein et al. 2007; Williams and Kremen, 2007). The habitat’s heterogeneity promotes biodiversity in human landscapes and hence may provide ‘biological insurance’ for services currently rendered by managed insect species (Ives et al. 2000; Winfree et al. 2007).

The aim of present study was: (1) to examine floral phenology in one of most showy ornamental species Geranium platypetalum, (2) to investigate floral rewards available to visiting insects and (3) to monitor the activity and spectrum of insects collecting these rewards. The primary purpose of this investigation was to determine the floral traits in G. platypetalum beneficial for relationships with visiting insects as well as to check if these plants can supply their flower visitors with an ample, high quality food during spring time, i.e. the period of high food demand by bees.

**MATERIALS AND METHODS**

**Study site and plant species**

The present study was conducted on a cultivated plot of G. platypetalum grown on a loess-origin soil in the Botanical Garden of Maria Skłodowska-Curie University, Lublin, Poland (N-51°09’, E -22°27’). The census plot occupied an area of 7 m². The observed plants grew in a dense patch so it was difficult to discriminate the individuals and to count their number. Geranium platypetalum Fisch. & C. A. Mey., synonymous with G. ibericum var. platypetalum (Fisch. & C. A. Mey.) Boiss., is a perennial herb, 25-57 cm tall, which is native to northeast Turkey, Caucasus, and northern Iran and cultivated since 1802. The stem is erect, leafy, herbaceous. Basal leaves in a rosette. Rootstock ± horizontal. The flowers are hermaphroditic, actinomorphic, disc-shaped, 3-4.5 cm in diameter, deep blue with red veins, clustered in a dichasial cyme with 2-flowered cymules. The sexual parts, consisting of a pistil and surrounding 10 stamens, stand straight in the center of flower. Anthers are blue-black and gynoecium is dark purplish.

**Phenology and abundance of flowering**

The study on phenology of flowering was carried out on the species level as well as flower level (Dafni, 1992). During the period 2009-2011 flowering onset and flowering termination were recorded to determine the timing and duration of flowering. Moreover, in the years 2009-2010 the dynamics of flowering per area unit was examined as well. For this purpose, prior to opening of the first flowers, 5 plots, each 50×50 cm in size were selected at random on the patch and marked. On each plot, daily or every second day, all new flowers that opened were counted and marked with a marker until blooming terminated. The values were recalculated per 1 m² area. The dynamics of flowering was expressed as the percentage of newly opened flowers on successive flowering days in relation to the total number of flowers eventually formed on the plot (100%). The total number of flowers was determined per 1 m² area as well as per inflorescence. Moreover, the development stages of G. platypetalum flowers were observed. Floral persistence was counted as the days from the opening to the falling of all petals. The length of flowering of a single inflorescence was determined, too.

**Floral reward measure**

Preliminary observations on localization of floral nectaries were conducted. After removing elements of the corolla and anthers, the whole glands from fresh material were examined under a stereoscopic microscope. Nectar productivity was examined in the years 2007, 2009-2010. To determine it, flower buds were
isolated in the field and nectar was collected from perfect flowers at two different stages of flower development: male stage ( )-flowers with full pollen presentation (Fig. 1), and the female stage ( )-flowers after pollen exposure with fully expanded stigmas (Fig. 2). The nectar was gathered using glass micropipettes and its amount was measured (in mg). A total of 22 and 18 samples for and stage, respectively, were collected during this study. Each sample contained nectar collected from 1 to 10 flowers. Nectar sugar concentration was measured with the Abbe refractometer. Then, nectar amount and sugar concentration of nectar were used to calculate the total sugar amount (in mg) secreted in nectar per 10 flowers of each stage.

The pollen mass available to insects was determined by the ether method (Warakomska, 1972). In the years 2007, 2009-2011, 6 samples of 50 mature anthers were collected each year. Pollen production was expressed in mg per 100 anthers = 10 flowers.

**Insect visitation**

In the years 2010-2011, insect visiting and foraging activity on G. platypetalum flowers was monitored throughout peak blooming period. The number of open flowers and number of working insects in a field of view (0.25 m²) were counted for 5 minutes, three times every hour, from 08.00 h to 18.00 h (GMT+2h). The counts were converted to a visiting rate (visits per flower×min⁻¹). Observation discriminated four insect categories: honey bees, bumblebees, solitary bees, others (flies, ants). Relative abundance and daily visitation pattern of these categories were determined.

**Data analysis**

Whenever possible, parametric statistical analysis was used on variables by applying standard analysis of variance procedures. When significant differences were stated, the ANOVAs were followed by the HSD Tukey test at =0.05 (Stanisz, 2006). Descriptive statistics were calculated and are presented as the means ± S.D. Data in figures are presented as the average values.

Differences in the nectar amount, nectar sugar concentration and total sugar amount in nectar between the floral stages and years of study were tested by means of two-way ANOVAs. Differences in the amount of pollen per 10 flowers between years of study were analysed by one-way ANOVA.

Non-normally distributed data, the total number of flowers/inflorescence and total flower number×m⁻² were compared with the Kolmogorov-Smirnov test while the life-span of a flower and an inflorescence were subjected to Kruskal-Wallis ANOVA and H-test for nonparametric data.

Data analyses were performed with STATISTICA v.7.1 (StatSoft Poland, Krakow).

Fig. 1. The male stage of G. platypetalum flower. Anthers shedding pollen are visible (arrow)
RESULTS

Flowering pattern, length of blooming and floral display

Under the climatic conditions of eastern Poland during the 2009-2011 seasons, blooming of the studied species began in late May and lasted until the end of the second part of June. The detailed dates of the seasonal flowering period for *G. platypetalum* are shown in Table 1. The time of blooming differed among the years of the study and was affected by weather conditions during the flowering period. Generally, high temperatures speeded up the blooming process in plants. The observations carried out in consecutive growing periods resulted in models of flowering dynamics for the observed patches of *G. platypetalum*. Figure 3a represents the flowering dynamics curve obtained in the 2009 season. The flowering of the patches lasted 4 weeks. Throughout the first eight days flowers developed at a slow rate, with less than 2.5% of the total number of flowers produced per 1 m² each day. Then, the process of opening flower buds intensified. Starting from the 9th day the rate of bud opening began to grow and, on average, 11 days after flowering commencement as many 25% of all flowers were developed on each patch. Peak flowering (when >50% of the total number of flowers were open) took place 15-16 days after the first open flower buds. At peak flowering, more than 5% of the total number of flowers opened per 1 m² each day. The percentage of newly open flowers fell below 4.5% only between 15th and 17th day due to a significant drop in air temperature combined with rain falls. Generally, in 2009 the period of most intense flowering fell in the 2nd and 3rd flowering week. At this peak blooming time, the percentage of open flowers per 1 m² area was 70.4%, on average. Towards the end of the flowering period of a patch one could see a significant decrease in the number of newly opened flower buds; their percentage relative to the total number of flowers per plant dropped to less than 2% during the last four days.

The flowering dynamics curve obtained in 2010 (Fig. 3b) differed significantly from that for 2009. The flowering period was one week shorter. At the beginning of flowering, the flower development rate was slow (up to 5% per day). But at the end of the 1st week of flowering, the rate of bud opening increased strongly. The flowering commencement period, terminated after 6 days, on average, after blooming onset; then, one day later, peak flowering occurred. The maximum percentage of open flowers per 1 m²×day⁻¹ was 37.7%. Peak flowers opening on the plant started at the end
of the 1st week of the blooming period and continued for the following week. During this period, 91% of the total flowers formed on the 1 m² patch were open. The termination of blooming started in the 3rd week of flowering.

Examining the flowering dynamics curves, i.e. the number of newly open flowers per census day for the duration of flowering, it can be stated that the flowering of the investigated species begins with a small number of flowers, then steadily or quickly reaches a peak with few local maxima before tailing off, leading to a skewed distribution. In 2009, the skewed shape of the flowering curve more approximates a symmetrical distribution (Fig. 3a).

The detailed data concerning the blooming abundance of studied species are shown in Table 2. The influence of the growing season on the number of flowers formed per inflorescence was significant. However, the total number of flowers×m² was similar for the years of the study. Flowering was facilitated by good temperature and moisture conditions both during the flowering period and in the period preceding it.

The life-span of a single flower was 3 days while a single inflorescence persisted 11 days, on average (Table 2). Perfect flowers of Geranium platypetalum exhibit incomplete protandry at the intrafloral level. The stigmas became receptive and exposed when anthers continued to shed pollen in a flower. Therefore, there is an overlap in the presentation of the pollen and stigmas. Anthers started to shed pollen 1-2 hours after bud opening whereas stigma presentation started the following day after a flower opened.

**Floral nectar secretion**

In a flower of Geranium platypetalum nectar is secreted by five phanarothetic-discoid nectaries. The characteristics of nectar produced by flowers in the male and female stage are shown in Tables 3 and 4. The amounts of nectar collected in the male and female phases differed significantly (Table 3). Flowers in the male stage produced by 40.8% more nectar, on average, when compared to the female stage flowers (Table 4). The sugar nectar concentration showed a significant stage and year effect (Table 3). In contrast to the nectar amount, the higher values were found for samples collected from the female stage flowers. The nectar collected in 2010 was more concentrated than that gathered in 2007 and 2009 – the mean sugar content exceeded 60%. Finally, the total nectar sugar amount secreted in nectar for both stages of flower development did not differ significantly (Table 3), however the values obtained for the male stage were slightly higher than those for the female stage. The year effect was significant (Table 3). In 2010, with the highest temperatures and sunny days during flowering of the species, nectar sugar yield increased twice to 2.5× when compared to 2009 and 2007.

**Pollen production**

The pollen output from 100 anthers (equal to 10 flowers) is shown Fig. 4. The mass of pollen did show a year effect (Table 3). Extremely low amounts were produced by flowers in 2010 whereas the highest values were found in 2007. The variation within species in the amount produced by the same number of anthers can be caused by differences in anther size and by the percentage of non-fertile pollen grains, which can vary from year to year. In Geranium platypetalum a tendency to produce even empty anthers was observed.

**Insect visitation**

Flowers of Geranium platypetalum attract numerous insect visitors. Under good weather conditions they visited flowers throughout a day with their peak activity between 10.00 and 14.00 hrs and the rate of visitation increased slightly after 17.00 h (Fig. 5). The daily visitation patterns of various groups of insects on Geranium flowers are shown in Figure 6. The insects gathered mainly nectar. In 2010 and 2011 the mean visiting rate was 0.152 and 0.145 visit per flower×min⁻¹, respectively. The visitor assemblage changed during the years of observations. The principal visitors were Hymenoptera and among them Apis mellifera dominated. In 2010 honey bee workers were the only visitors observed on Geranium flowers while in 2011 they comprised 86.6% of all insects observed. Moreover, the flowers were visited by a number of bumblebees, solitary bees, flies and ants (Fig. 7).

**Table 1.**

Dates of flowering and length of flowering period of *Geranium platypetalum* in the years 2009-2011

<table>
<thead>
<tr>
<th>Year</th>
<th>Flowering period</th>
<th>Length of flowering period (in days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>30 May – 26 June</td>
<td>28</td>
</tr>
<tr>
<td>2010</td>
<td>28 May – 22 June</td>
<td>26</td>
</tr>
<tr>
<td>2011</td>
<td>25 May – 17 June</td>
<td>24</td>
</tr>
</tbody>
</table>
Fig. 3. Seasonal dynamics of blooming of *G. platypetalum* in the years 2009 (a) and 2010 (b). Means are given.
Fig. 4. Pollen mass produced per 100 anthers (10 flowers) *Geranium platypetalum* in mg during the years of study. Means are given (n=6 for each year). Vertical bars indicate S.D. around the means. Values with the same letter do not differ significantly at = 0.05. HSD Tukey test was used.

Fig. 5. Daily pattern of insects activity on *Geranium platypetalum* flowers. Means are given.
Fig. 6. Daily pattern of the different groups visiting *G. platypetalum* flowers, shown as relative abundance in %, in 2011 season. Mean values are given.

Fig. 7. Relative abundance of insects visiting flowers of *G. platypetalum* in Lublin area in 2011 season. Mean values are given.
Table 2.
Year effect on abundance of flowering and persistence of flowers and inflorescences in *G. platypetalum* studied during the years 2009-2011. Values are means ± S.D. (n)

<table>
<thead>
<tr>
<th>Variable</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>P – values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of flowers per inflorescence</td>
<td>11.42±5.0 (101)</td>
<td>16.24±5.09 (87)</td>
<td></td>
<td>P &lt; 0.02 *</td>
</tr>
<tr>
<td>Number of flowers per 1 m²</td>
<td>1146.4±122.5 (5)</td>
<td>1130.2±695.8 (5)</td>
<td></td>
<td>P &gt; 0.1 ns</td>
</tr>
<tr>
<td>Lifetime of a single flower (days)</td>
<td>2.67±0.49 (12)</td>
<td>2.90±0.45 (19)</td>
<td>3.03±0.18 (30)</td>
<td>P = 0.0151 *</td>
</tr>
<tr>
<td>Lifetime of an inflorescence (days)</td>
<td>10.99±2.79 (87)</td>
<td>11.41±1.56 (12)</td>
<td></td>
<td>P &lt; 0.002 **</td>
</tr>
</tbody>
</table>

The Kolmogornov-Smirnov test was performed for the number of flowers per inflorescence, number of flowers per 1 m² and lifetime of an inflorescence whereas for the life time of a single flower the Kruskal-Wallis test was used. Statistical differences are noted: ** P<0.01, * 0.01<P<0.05, ns P>0.05

Table 3.
ANOVA’s of the effects of flower stage (  or ) and year of study on nectar, and pollen productivity in *G. platypetalum* during the years of study.

<table>
<thead>
<tr>
<th>Variable</th>
<th>df</th>
<th>Nectar amount per 10 flowers</th>
<th>Sugar content of nectar</th>
<th>Total sugar mass per 10 flowers</th>
<th>Pollen mass per 100 anthers (10 flowers)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Stage</td>
<td>1</td>
<td>1064.2</td>
<td>4.780*</td>
<td>600.6</td>
<td>5.13*</td>
</tr>
<tr>
<td>Year</td>
<td>2</td>
<td>26.1</td>
<td>0.117</td>
<td>2878.1</td>
<td>24.60***</td>
</tr>
<tr>
<td>Stage x year</td>
<td>2</td>
<td>182.2</td>
<td>0.819</td>
<td>67.0</td>
<td>0.57</td>
</tr>
<tr>
<td>Error</td>
<td>34</td>
<td>222.7</td>
<td>117.0</td>
<td>12.20</td>
<td></td>
</tr>
</tbody>
</table>

Significant effect: * P<0.05, ** P <0.01, *** P<0.001; ns = not significant; ¹ values for pollen mass

Table 4.
Amount of nectar (mg), sugar content of nectar (% wt/total wt) and total sugar mass in nectar (mg) in the male and female stage of *G. platypetalum* flowers during the years 2007, 2009-2010. Values are means ± S.D.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Year</th>
<th>No. of samples</th>
<th>Nectar amount per 10 flowers</th>
<th>Sugar content of nectar</th>
<th>Total sugar mass per 10 flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male ( )</td>
<td>2007</td>
<td>10</td>
<td>32.5 ± 18.53</td>
<td>23.90 ± 5.97</td>
<td>7.20 ± 2.71</td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>8</td>
<td>31.88 ± 22.08</td>
<td>18.35 ± 15.13</td>
<td>8.56 ± 8.99</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>4</td>
<td>25.00 ± 10.55</td>
<td>59.50 ± 7.65</td>
<td>14.88 ± 3.39</td>
</tr>
<tr>
<td>Mean for stage</td>
<td>22</td>
<td>29.79 ± 18.66 A</td>
<td>33.92 ± 15.03 A</td>
<td>10.21 ± 5.97 A</td>
<td></td>
</tr>
<tr>
<td>Female ( )</td>
<td>2007</td>
<td>4</td>
<td>11.75 ± 6.63</td>
<td>36.10 ± 2.54</td>
<td>4.37 ± 2.70</td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>8</td>
<td>17.82 ± 5.41</td>
<td>31.30 ± 16.75</td>
<td>5.86 ± 3.73</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>6</td>
<td>23.34 ± 2.98</td>
<td>61.75 ± 0.22</td>
<td>14.44 ± 1.79 A</td>
</tr>
<tr>
<td>Mean for stage</td>
<td>18</td>
<td>17.64 ± 6.45 B</td>
<td>43.05 ± 17.78 B</td>
<td>8.21 ± 5.24</td>
<td></td>
</tr>
<tr>
<td>Mean for the year of study</td>
<td>2007</td>
<td>14</td>
<td>21.13 ± 18.61 a</td>
<td>30.00 ± 7.57 b</td>
<td>5.78 ± 2.91 b</td>
</tr>
<tr>
<td></td>
<td>2009</td>
<td>16</td>
<td>24.85 ± 17.14 a</td>
<td>24.83 ± 16.81 b</td>
<td>7.21 ± 6.79 b</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>10</td>
<td>24.17 ± 2.64 a</td>
<td>60.63 ± 1.06 a</td>
<td>14.64 ± 1.53 a</td>
</tr>
</tbody>
</table>

Means in columns with the same letters are not significantly different at =0.05. The HSD Tukey test was used.


DISCUSSION

In the environmental conditions of central Europe as well in the region of its origin G. platypetalum blooms from May until August (Marcinkowski, 2002; Aedo et al. 2007). In the present study the flowering period of this species was much shorter and usually terminated before the end of June. The differences in the length of flowering can be caused by heterogenous environmental conditions (e.g. soil type and weather conditions), differences among genotypes, or phenotypic plasticity (Rathcke and Lacey, 1985; Elzinga et al. 2007).

Plants differ greatly with respect to their patterns of flower presentation. Some species boom during a brief period and have many open flowers, whereas others have extended flowering with only a few open flowers at one time (Gentry, 1974). In G. platypetalum the models of flowering phenology changed in the successive years of study. When analyzing the obtained flowering curves the plant patches show continuous flower development and demonstrate a ‘cornucopia’ pattern of flowering sensu Gentry (1974), and a positively skewed distribution according to Thomson (1980) in 2009, with a tendency towards a more symmetrical curve in 2010. Subhadrabandhu et al. (1978) found that the pattern of flower production in Phaseolus vulgaris varied from a concentrated skewed pattern to a longer and more normally distributed pattern. Gentry (1974) pointed out that the great majority of temperate, generalist plants employed ‘cornucopia’ strategy. Thomson (1980, 1985) as well as Forrest and Thomson (2009) suggest that selection favoured asymmetrical, positively skewed curves. By displaying numerous flowers from the beginning of bloom, the plant obtains the services of faithful visitors that will continue to visit despite subsequent decreases in the rate of flower production (Thomson, 1985). The observed differences in the flowering curves of G. platypetalum reflect a high susceptibility of this species to weather conditions prevailing in the blooming period. Generally, the opening of new flowers intensified in the 2nd week of flowering as it was previously observed in G. sanguineum (Masierowska, 2006).

The studied species produced numerous flowers; their density per 1 m² exceeded 1100 flowers. Similar values were found for G. sylvaticum (Jabłoński and Koltowski, 2002). However, significant differences between the years of study were found only for the of number of flowers in a single inflorescence. The abundance of blooming may be influenced by weather conditions during the vegetation period, as was observed during this study.

Flowers of G. platypetalum show a typical entomophilous character offering to insects both nectar and pollen. However, nectar is the main reward collected by them. In the flowers of this taxon the secretory tissue forms five glabrous nectaries at the bases of the episepal filaments of the anthers, between the petal insertion. According to Link (1990), this is a phanerothetic-discoid gland type, commonly occurring in the Geranium genus. The arrangement of floral elements in Geranium flowers makes nectar easy accessible to various insect visitors.

Flowers of G. platypetalum exhibit incomplete protandry based on the criteria of Lloyd and Webb (1986). This kind of dichogamy occurs commonly in the Geraniaceae family and is regarded as one of the mechanisms to avoid selfing and to promote outcrossing in these plants (Fægri and van der Pijl, 1980; Zomler, 1994; Kandori, 2002; Asikainen and Mutikainen, 2005). According to Fitz et al. (2008), G. platypetalum is a xenogamous species.

In the present study clear differences in nectar yield occurred during the two sexual phases within a flower. The male phase averaged 1.7-fold as much nectar and a similar nectar-sugar amount as the female phase did. In contrast, the sugar content in nectar was much higher in the female stage, compensating the differences in the secreted amounts of nectar. The results of this study are difficult to compare because the relevant data concerning nectar production in different stages of flower development in G. platypetalum or another Geranium species are lacking. In contrast, in the protandrous flowers of Carum carvi, Apiaceae (Langenberger and Davis, 2002) and Echinacea purpurea, Asteraceae (Wist and Davis, 2006), the highest average values of the nectar amount, nectar-solute concentration as well as nectar-sugar quantity occurred in the pistillate–stage florets when nectar becomes the major reward available in flowers. In the female stage of G. platypetalum flowers nectar attractiveness improved mainly due to a 1.7-fold increase in nectar concentration which exceeded 61%. The high concentration of nectar in Geranium species was previously described by Maurizio and Graf (1969), Jabłoński and Koltowski, 2002; and Masierowska (2006).

The discrepancies in a pattern of nectar production in a protandrous species obtained by Davis and co-workers and in the present study can be attributed not only to a species effect but also to diverse conditions in which those experiments were conducted. The Carum and Echinacea plants were grown in a growth chamber, whereas in the present investigations nectar samples were collected directly from the plants grown in the field. To explain the different tendency in the nectar secretion pattern a more detailed study under controlled conditions is necessary.
Overall, the nectar yield from 10 flowers of *Geranium platypetalum* was not very high and the nectar-sugar quantities were in the range of the values obtained for *G. collinum* (Míkóv, 1974) or *G. sanguineum* (Masierowska, 2006). Throughout the whole lifetime – that means that nectar was collected at the end of the female stage – ten flowers of these species secreted 3-18 mg and 4.7-14.8 mg of sugar in nectar, respectively. Both these taxa are considered to be valuable melliferous plants but they secreted nectar abundantly and regularly only under high air humidity and air temperature – similarly to *G. platypetalum*.

The pollen output from 10 flowers of *G. platypetalum* was 19.06 mg and it was lower when compared to mean pollen productivity of 10 flowers of *G. sanguineum* (Masierowska, 2006). According to Maurizio and Graf (1969), crane’s bills can provide 1-3% of pollen yield in mountain areas. But interestingly, in the male phase of *G. platypetalum*, flowers the visitors concentrated on nectar and did not actively gather the released pollen. Large insects collecting nectar such as *A. mellifera* and Bombus spp. were usually located upon the sexual parts and deposited pollen on their abdominal side (sternotribic pollen deposition) while small insects were often located on the peripheral petals, walking on them and having much less contact with the anthers. Similar behavior was previously described in some *Geranium* species by Kandori (2002) and Kozuharova (2002).

The phenotypic generalization of *G. platypetalum* flowers, including easily accessible nectar rewards, welcomes an array of insect visitors, e.g. bees, flies and ants. The present observations showed that although the pollinator assemblage differed in the successive years of study, the key visitors were hymenopterans, mainly honey bees. Honey bees as the most abundant visitors in *Geranium* flowers as well as the presence of bumblebees and wild bees from the Andrenidae, Halictidae and Megachilidae families were reported in several studies, e.g. Kandori (2002), Masierowska (2006), Fiz et al. (2008). Also syrphids and ants were listed among flower visitors in these plants. The mean total number of visits per flower×min−1 for *G. platypetalum* was higher when compared to *G. plumeum* or *G. sylvaticum* (reviewed in Fiz et al. 2008) – wild and sometimes cultivated species eagerly visited by bees. The intensity of visits is an important factor influencing the pollination success. In general, the greater the visitation intensity, the higher the chance of pollination; however, numerous studies have shown that insects with high visitation rates could be poorer pollen depositors (Engel and Irwin, 2003). Insect visit frequency changed over the course of a day. The pattern of daily activity of flower visitors was associated with the opening of new flowers as well as with floral rewards availability.

CONCLUSIONS

*Geranium platypetalum* exhibits several floral traits beneficial for insect visitors at both population and intrafloral levels including the flowering pattern, floral display and floral rewards. In the course of this study these plants were observed to be a highly valuable source of nectar flow, especially for hymenopterans during spring. Increased planting of *G. platypetalum* in naturalistic parks and gardens is recommended in order to achieve excellent ornamental effect as well as to enrich the nectar pasture for *A. mellifera* and wild Apoidea.

Acknowledgements

Research supported by the Ministry of Science and Higher Education of Poland as part of the statutory activities of the Department of Botany, University of Life Sciences in Lublin.

REFERENCES


Floral phenology, floral rewards and insect visitation in an ornamental species Geranium platypetalum Fisch. & C. A. Mey...


Fenologia kwitnienia, nagrody kwiatowe i oblot przez owady ozdobnego gatunku Geranium platypetalum Fisch. & C. A. Mey., Geraniaceae

Streszczenie
W ciągu 4 lat badano fenologię i sezonową dynamikę kwitnienia, wielkość oferty kwiatowej oraz sekcję nektaru i obfitość pylenia u G. platypetalum Fisch.& C. A. Mey. Ponadto obserwowano oblot kwiatów tego gatunku przez owady.

Kwitnienie roślin trwało od końca V do końca VI. Krzywa kwitnienia ma rozkład skośny z tendencją do krzywej normalnej. Wielkość oferty kwiatowej zmieniała się w czasie okresu kwitnienia. Najintensywniejsze rozwijanie kwiatów miało miejsce w drugim i trzecim tygodniu kwitnienia. Kwiaty G. platypetalum są protandryczne, fazy i częstoowo zazębiają się.

Produkcja nektaru w obu stadiach różni się istotnie. Dziesięć kwiatów w stadium i wydzielano średnio 29.8 mg i 17.6 mg nektaru, o przeciętnej koncentracji cukrów odpowiednio, 33.9 % i 43.1 %. Średnia masa cukrów wydzielonych w nektarze nie różniła się istotnie i wynosiła 10.2 mg i 8.2 mg. Dziesięć kwiatów G. platypetalum produkowało średnio 19.06 mg pyłku.

Kwiaty G. platypetalum odwiedzały głównie pszczoły (Apoidea). Szczytowy oblot kwiatów miał miejsce pomiędzy 10.00 h a 14.00 h. Głównym zbierającym pozytkiem był nektar. Średnia intensywność odwiedzin pojedynczego kwiatu×min⁻¹ wyniosła 0.149.

Nasadzanie roślin G. platypetalum w parkach i ogrodach może wzbogacić pożytek nektarowy owadów pszczolowatych.