

ADAPTATIONS OF *Lamium album* L. FLOWERS TO POLLINATION BY APOIDEA

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Abstract. The presence of ruderal and mid-field vegetation promotes conservation of biodiversity and provides an additional source of food for insect pollinators. The white dead-nettle is a common synanthropic plant visited frequently by various groups of insects, as it is a source of pollen and nectar. In 2012–2013, in the city of Lublin (Poland), signalling and food attractants in *L. album* flowers were analysed using light and scanning electron microscopy. The pipetting method was used for determination of nectar abundance in the flowers, and the content of sugars in the nectar was assessed with the use of an Abbe refractometer. It was found that the white dead-nettle flowers emitted a fragrance and were equipped with nectar guides, and the corolla and stamens had glandular trichomes and papillae secreting essential oils. On the stamens, there are also non-glandular trichomes, which play a role of pollen presenters. The nectary in the *L. album* flower has a shape of an irregular disc partly surrounding the base of the ovary. The content of sugars in the nectar was 43%. Sugar and honey yields per ha were calculated, and the values obtained were 153 kg and 191 kg, respectively.

Key words: white dead-nettle, nectary and nectar, trichomes, pollen presenter, sugar yield

INTRODUCTION

Lamium album L. is one of the 6 species of the genus *Lamium* occurring in Poland. This common synanthropic weed can be found near rock debris sites, roadsides, fences, midforest clearings, and in brushwood [Rutkowski 2006]. *L. album* flowers have medicinal properties and they are used as herbal anti-inflammatory and coating agents [Lamer-Zarawska et al. 2007]. The flowers are characterised by abundant and long-term flowering, between April and September, or sometimes November. White dead-nettle plants produce creamy-white, two-lipped, entomophilous flowers. They are frequently visited by insect pollinators (primarily bumblebees, honeybees and wild bees) attracted by the nectar and pollen reward, which contribute to cross-pollination of these plants

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[Denisow and Bożek 2008, Cozmuta et al. 2012]. Some authors report that Lamiaceae flowers produce great amounts of nectar stored deep in the corolla tube; therefore, they may mainly be visited by long-tongued bees, sphingid and noctuid moths, butterflies with high wing loading, and a few syrphids and bombyliids [Corbet 2006]. Maurizio and Grafl [1969], Petanidou et al. [2000] and Petanidou [2005] found a high concentration of sugars, dominated by sucrose, in the nectar of Lamiaceae representatives. According to the data reported by Bodnarčuk et al. [1993], *L. album* nectar is not only rich in sugars, but also aromatic.

Maurizio and Grafl [1969] described the *Lamium* nectary as an irregular disc surrounding the ovary base. The authors observed that nectar secreted by *Lamium* was protected against rain by trichomes located in the corolla throat. Gulyás [1967] described the nectary of this taxon as an asymmetric gland with a better-developed part at the lower lip. In turn, Vogel [1983] found that the nectariferous disc in the flowers continued secreting nectar for a while after the corolla was shed.

The ruderal plants promote conservation of biodiversity and are a source of food for insect pollinators, therefore the aim of the study was to evaluate insect signal and food attractants in *L. album* flowers, including colourful patches, odour-emitting structures, pollen presentation, and nectar abundance. Additionally, preliminary analyses of the morphology of flower nectaries were carried out.

MATERIAL AND METHODS

The research material included white dead-nettle (*Lamium album* L.) plants growing in a synanthropic community in the Śródmieście district of Lublin (51.24°N and 22.57°E, Poland).

The number of flowers was evaluated in 25 randomly selected *L. album* plants. Using a stereoscopic microscope SMT 800, measurements of flower parts were performed. The length of the calyx (at the longest point) and corolla, the length of the corolla tube at its widest point, and the length of stamens (filaments and anthers) were measured (n = 20 flowers). The height (at the highest point) and the external diameter of the nectaries (n = 20) as well as the length of trichomes located on the abaxial epidermis of the upper lip and on the adaxial epidermis of the corolla tube (n = 20) were measured. Photographs of the flowers and their fragments were taken.

The micromorphology of *Lamium album* L. flower elements was analysed under a scanning electron microscope. Sections of the calyx, corolla, stamens, pistils as well as dissected nectaries and pollen grains were fixed in 4% glutaraldehyde in 0.1 M phosphate buffer, pH 7.0, at temperature of 4°C. After dehydration in ethanol and an acetone series, the plant samples were dried at liquid CO₂ critical – point and sputtered with gold. Observation and photographic documentation were performed using a scanning electron microscope Tescan Vega II LMU. The size of the pollen grains was assessed in semi-permanent glycerol-gelatine slides. The length of the polar axis and equatorial diameter of swollen pollen grains (n = 100) was measured. The shape of the pollen grains was assessed on the basis of the ratio of the polar axis (P) to the equatorial diameter (E) [Dybova-Jachowicz and Sadowska 2003].

In 2012–2013, the abundance of flowering and nectar secretion of *Lamium album* L. flowers were estimated and the flower life span was evaluated. Nectar was sampled with the pipette method [Jabłoński 2003]. In total, 18 samples were collected. One sample contained nectar produced by 4–30 flowers. The nectar was collected throughout the life span of the flowers. The percentage content of sugars in the nectar was determined using an Abbe refractometer. The mean mass of sugars contained in the nectar from 10 flowers was calculated. On the basis of the mean mass of nectar sugars and flowering abundance, sugar yield and honey yield were calculated.

Data on the nectar mass and the concentration and mass of sugars contained therein were analysed by the two-way analysis of variance. The significance of the differences between the means was determined using the Tukey's T test at the significance level $\alpha = 0.05$. Standard deviations for the variables were calculated. The correlations between the variables were presented by the Pearson correlation coefficient. The calculations were performed using Statistica 6.0 program.

RESULTS

Our observations indicate that *Lamium album* L. flowers in Poland are visited by both, bumblebees and honeybees (figs 1 A, B).

Corolla signal attractants. *L. album* flowers emerge from leaf axils in pseudo-whorls composed of 5–22 flowers, thus forming a characteristic inflorescence (fig. 1 A). One plant produces 16–119 flowers (mean 56). The flower consists of a campanulate, 8–12-mm-long, green calyx with 5 elongated teeth surrounding the corolla base (fig. 1 D). The white 2-lipped corolla reaches a length of 19–21 mm. The surface and edges of the helmet-like upper lip is covered by trichomes with a length of 200–565 μm (figs 1 A–C). The lip protects the stigma and pollen-releasing anthers. The lower lip bears 3 lobes; the largest central lobe exhibits symmetrically arranged yellow-green spots on its surface. They form a characteristic picture, which is an indicator of nectar (nectar guides) for insect pollinators (figs 1 A, C, E). The lateral lobes of the lower lip are equipped with elongated teeth (fig. 1 C), which enable insects to remain on the flower. The upper surface of the lower lip emits a gentle fragrance thanks to the presence of essential oils both released from capitate secretory trichomes and produced by the epidermis of appendages called papillae (fig. 1 F). The 6.8–8.6 mm long and 2.6–3.1 mm wide corolla tube is curved and dilated below the lower lip (fig. 1 D). Inside the corolla tube, 3–5 mm above the nectaries, there is an oblique half-ring of white trichomes (283.1 – 428.5 μm length) located on the lower lip side (fig. 2 A). The trichomes are viable, slightly flattened, and sharply pointed (figs 2 A, B, E). The adaxial surface of the corolla tube bears conical trichomes and its central part exhibits dilated hairs, which probably participate in fragrance emission, as secretion residues were observed on their surface (figs 2 A, C, D, F, G). The adaxial epidermis of the corolla tube has capitate trichomes, which also take part in odour emission (figs 2 A, D).

Attractants located on the stamens. The androecium in *L. album* flowers is composed of 4 stamens, 2 of which are longer with anthers located higher (fig. 3 A). The length of the longer and shorter stamen filaments is 8.4–12.8 mm and 5.8–7.0 mm, respec-

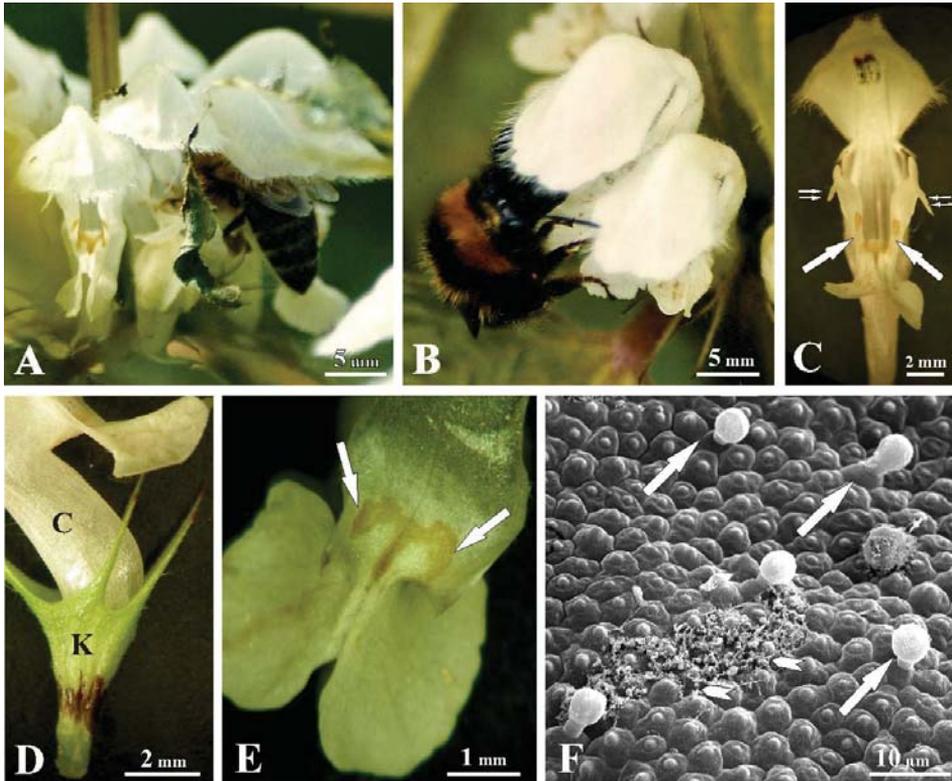


Fig. 1. The flower and elements of the perianth in *Lamium album*. A – Fragment of the inflorescence with a visible *Apis mellifera* forager; B – Representative of the genus *Bombus* in a white dead-nettle flower; C – Corolla with distinct nectar guides (arrows) and teeth on the lobes of the lower lip (double arrows); D – Fragment of the lower part of the corolla tube (C) and calyx (K); E – Central lobe of the lower lip constituting a “landing site” for insect pollinators. The arrows indicate a colour spot; F – Fragment of the adaxial surface of the upper lip covered by papillae. Visible capitate glandular trichomes (arrows) and secretion (arrowheads) (phot. A. Sulborska)

tively, whereas the length of the anthers is similar, i.e. 1.5–1.9 mm and 1.6–1.8 mm. The anthers are black, strongly hairy (figs 3 A, B). Long, viable trichomes emerge near the anther dehiscence slit, through which pollen is released. Convex thickenings of the cell wall are formed on the surface of the trichomes. Clusters of pollen grains covered by a layer of pollen glue are attached to the trichomes (fig. 3 C).

The stamens of *L. album* flowers, the same as the corolla petals, emit a scent. Essential oils are produced in the capitate secretory trichomes present in the filament epidermis (fig. 3 B). The discharge is also secreted by multicellular trichomes on the anther surface (figs 3 B, D). We observed pollen grains attached to some secretory trichomes, which must have been facilitated by the secretion released by the trichomes (fig. 3 D).

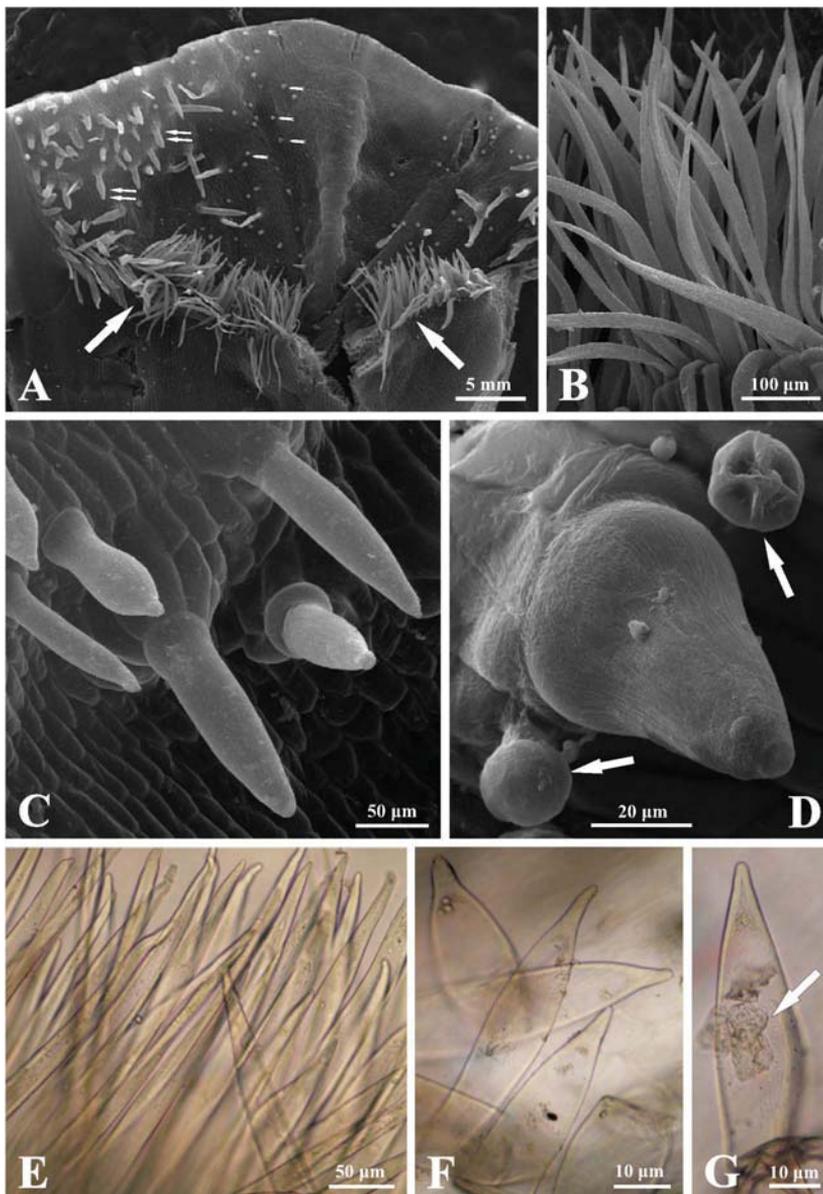


Fig. 2. Micromorphology of elements of the *Lamium album* corolla. A – Fragment of the lower part of the corolla tube with a visible half-ring of long trichomes (arrows) and with conical (double arrows) and capitate (arrowheads) glandular trichomes; B, E – Trichomes forming a half-ring in the lower part of the corolla tube viewed under SEM (B) and a light microscope (E); C – Fragment of the inner surface of the corolla tube with visible glandular trichomes; D – Conical glandular trichome from the adaxial surface of the corolla tube and capitate trichomes (arrows); F, G – Conical glandular trichomes from the inner part of the corolla tube. The arrow in photograph G indicates secretion (phot. A. Sulborska)

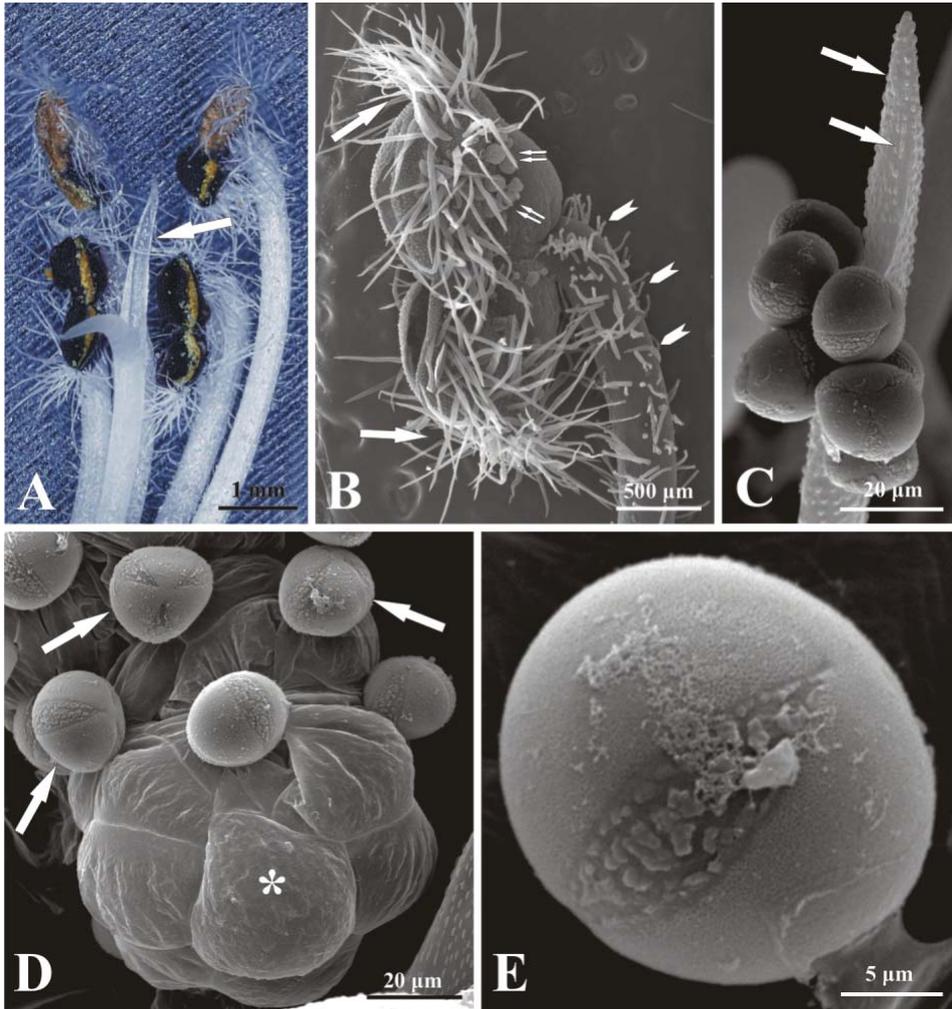


Fig. 3. *Lamium album* androgynium and pollen grains. A – Upper fragments of stamens and the style with the stigma (arrow); B – Fragment of stamen. Visible pollen presenters (arrows), multicellular glandular trichomes on the filaments (arrowheads), and peltate glandular trichomes on the anther (double arrows); C – Apical part of a trichome from the pollen presenter with visible thickenings of the cell wall (arrows) and attached pollen grains; D – Peltate glandular trichome (asterisk) from the surface of the anther and pollen grains (arrows); E – Pollen grain in the equatorial view (phot. A. Sulborska)

Morphology of the pollen grains. *L. album* pollen grains can be classified as medium-sized, due to the length of the polar axis (P) reaching 25.8 μm and the length of the equatorial axis (E) equal to 24.2 μm . In terms of the shape, the pollen grains are *prolato-spheroides* ($P/E = 1.07$).

The grains have three colpi and are triangular in the polar plane but elliptical and slightly flattened in the equatorial plane. The surface of the exine in the intercolpia contains micropores, whereas the exine within the colpi is irregularly granular with distinct clusters of granules (figs 3 C–E).

Morphology of the nectaries. The nectar gland in the *L. album* flower is light creamy to yellow in colour and has a shape of an irregular disc partly surrounding the ovary (figs 4 A, B). The ovary is green and consists of four apically concave parts (fig. 4 A). The height of the nectary at the highest point reaches, on average, 513 μm . The outer diameter of the gland is 965 μm . The epidermal cells of the nectary have irregular shapes. Their outer wall is covered by a smooth cuticle (fig. 4 C).

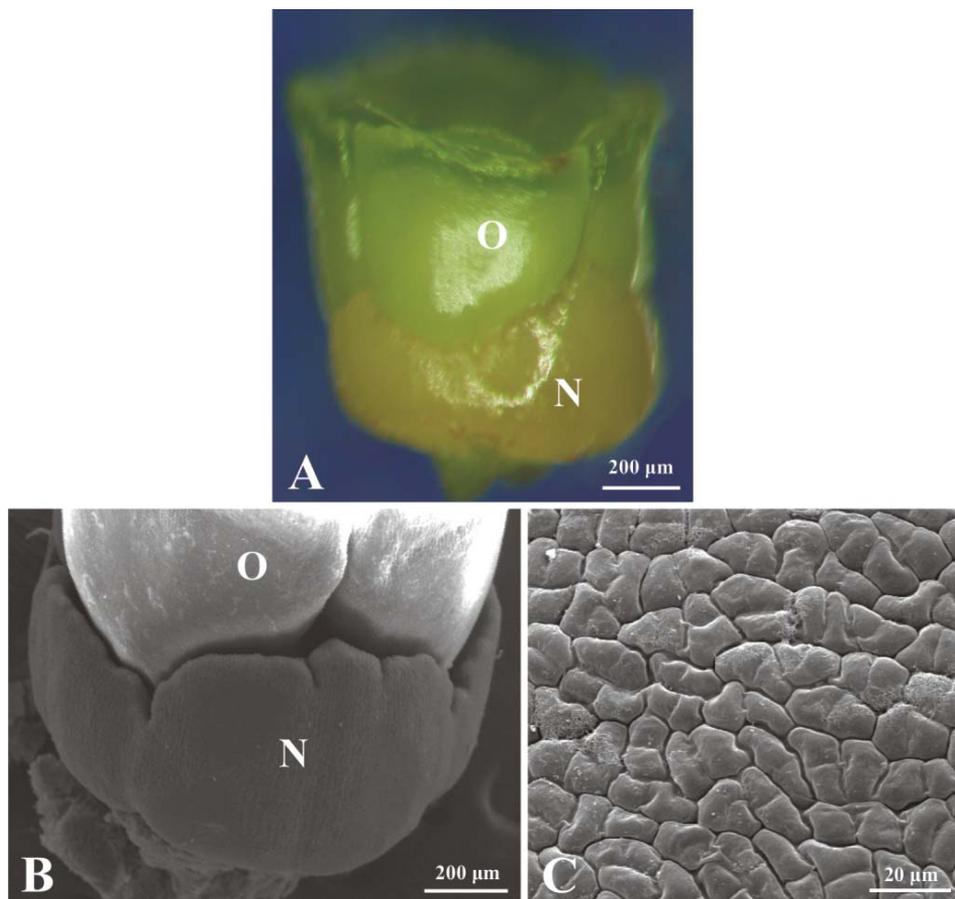


Fig. 4. *Lamium album* ovary and nectary. A – Ovary (O) with a visible yellow nectary (N); B – Fragment of the ovary (O) and nectary (N); C – Surface of the nectary viewed under SEM (phot. A. Sulborska)

Table 1. Amount of nectar, sugar content of nectar and total sugar mass in nectar per 10 flowers of *Lamium album* L. in 2012–2013. Values are means \pm SD

Year	Term	No. of samples	Nectar amount mg	Sugar concentration in nectar, %	Total sugar mass mg
2012	1.	2	19.85 \pm 0.33a	35.10 \pm 0.14bc	6.97 \pm 0.12b
	2.	3	34.07 \pm 0.98a	41.75 \pm 9.25abc	13.82 \pm 0.34ab
	3.	3	38.47 \pm 1.32a	49.47 \pm 4.05ab	18.91 \pm 0.64ab
	4.	2	38.70 \pm 1.87a	51.65 \pm 2.05a	19.80 \pm 0.88 a
	mean		32.77A	44.49A	14.88A
2013	1.	5	28.10 \pm 0.34a	53.76 \pm 4.39a	15.05 \pm 0.16ab
	2.	3	26.00 \pm 0.88a	29.50 \pm 4.27c	7.69 \pm 0.31ab
	mean		27.05A	41.63A	11.37A
Mean		29.91 \pm 1.02	43.06 \pm 10.29	13.13 \pm 0.58	

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

Nectar abundance. Nectar production in *L. album* was investigated in 2012 and 2013. On average, one flower lived for 3–4 days. The average nectar production during the 2 years was 29.9 mg; in 2012 it was 21% higher than in 2013 (tab. 1). The content of sugars in the nectar analysed during the two years was similar with a mean of 43%. In turn, the mass of sugars produced throughout the life span of 10 flowers was about

Table 2. Nectar production of *Lamium album* in studies of various authors

Authors	Nectar amount per 1 flower, mg	Sugar content of nectar, %	Total sugar mass per 1 flower, mg	Honeyyield, kg \cdot ha ⁻¹
Sulborska, Dmitruk, Konarska, Weryszko-Chmielewska	2.99	43.06	1.31	191
Bodnarćuk et al. 1993	–	–	0.3–0.5	20–150
Maurizio and Graf, 1969;	2.0–2.7	29–38	0.7–1.3	173–203
Gulyás, 1967	1.5	46.1	0.69	–
Jabłoński, 1960	2.56	52.8	1.35	173–208
Demianowicz, 1953	–	–	–	100

13 mg (tab. 1). A strong positive correlation was found between the nectar weight and the sugar mass ($r = 0.87$, $p < 0.001$) and between the percentage content of sugars in the nectar and the sugar weight ($r = 0.60$, $p < 0.01$). The mass of sugars obtained from 1 white dead-nettle shoot producing on average 56 flowers was 73.53 mg. Sugar and honey yields per ha were calculated, and the values obtained were 153 kg and 191 kg, respectively (tabs 1, 2).

DISCUSSION

Flowers present sensory signals by which insects choose reward sites. These signals can be synergistic and complementary to enable pollinators to find flowers in different environmental conditions. Floral phenotypes are characterized by colour, scent, size, and shape, which are putatively associated with specific pollinator classes [Fenster et al. 2004, Raguso 2004].

Flowers pollinated by Apoidea do not exhibit a single characteristic pollination syndrome. Most frequently, bees prefer yellow, blue, and purple flowers with well-defined three-dimensional e.g. tubular, campanulate, or zygomorphic shapes [Proctor et al. 1996]. According to another author, when faced with different colours of flowers, the honeybee prefers visiting yellow, intensely blue, and white flowers [Harborne 1997]. It can be assumed that the white colour together with the yellow-green picture, delicate scent, as well as the size and shape of the *L. album* corolla constitute “syndromes” adapting the flowers to pollination by Apoidea.

The characteristic structure of the two-lipped corolla with reduced lateral lobes of the lower lip is typical for species from the *Lamium* genus [Rutkowski 2006]. In *L. album* flowers, the lateral lobes of the lower lip are equipped with sharp teeth, which support the legs of visiting insect pollinators.

We observed nectar and pollen honeybee foragers and bumblebees in *L. album* flowers. Various authors report that flowers of this species are mainly pollinated by bumblebees as well as honeybees and other insects [Lye et al. 2009, Cozmuta et al. 2012]. Denisow and Božek [2008] reported that bumblebees dominated among the flower-visiting insects (70–86%), whereas honeybee foragers accounted for 5.0–18.8%.

Scent attractants, weakly perceptible by the human sense of smell, are released in different parts of the *L. album* flower. This is related to the distribution of secretory structures on both the corolla petals and the surface of stamens. Various types of secretory trichomes and papillae were observed on petals and the corolla tube. Additionally, capitate trichomes secreting essential oils were noted on the filaments. Secretory trichomes of this type are characteristic for the representatives of the Lamiaceae family; they were also described in the flowers of other species from this family by other researchers [Bosabaldis and Tsekos 1982, Schulze et al. 1992, Dmitruk and Weryszko-Chmielewska 2010].

Trichomes covering flowers and retaining pollen grains released from anthers and thereby presenting pollen to insects, are called pollen presenters [Ladd 1994]. Our observations indicate that this function can be attributed to the trichomes present on *L. album* anthers.

Scent-emitting trichomes attract insects over long and short distances. It was found that different types of secretory trichomes in one taxon produce different secretions [Giuliani and Maleci Bini 2008]. Additionally, the different flower parts (calyx, corolla, stamens) emit fragrances of different quality [Pellmyr et al. 1987, Schulze et al. 1992, Farré-Armengol et al. 2013]. Proctor et al. [1996] found that the honeybee sensed 10–100 fold weaker odour concentrations than those perceived by the human sense of smell and differentiated even slightly differing scents. To date, the criteria for a success in metabolic engineering of the floral scent have been based on sensory evaluations by

humans, whose the odour threshold perception is much lower than that of most animals or insects [Vosshall 2000, Stockhorst and Pietrowsky 2004].

Kugler [1970] reported that *L. album* flowers emit a faint odour only in the lower lip, where the nectar colour indicators are located. However, our observations suggest that the essential oil is also emitted by trichomes distributed on the stamens and inside the corolla tube. In the case of *L. maculatum*, Kugler [1970] found that both flower lips had a similar scent, but the odour produced by the lower lip bearing colour indicators of nectar was stronger. The quality of the scent produced by the other corolla parts was different.

The sizes of the *L. album* pollen grains measured by us were (P) $25.8 \times 24.2 \mu\text{m}$ (E), with P/E = 1.07. These results differ from those reported by Denisow and Bożek [2008], who showed sizes of pollen grains equal to $29.38 \times 25.13 \mu\text{m}$ with P/E = 1.17, and by Beug [2004], where sizes were 22.5–30.3 μm , with the mean of 27.1 μm .

The maximum height of the *L. album* nectary reported in this study was, on average, 513 μm at the corolla length of 20 mm. This value is comparable with data obtained for other representatives of Lamiaceae: *Ocimum basilicum* (563 μm) and *Hyssopus officinalis* (626 μm), of which flowers were considerably smaller (9.6 mm and 11.9 mm, respectively) [Weryszko-Chmielewska 2000, Mačukanović-Jocić et al. 2007]. In contrast, the *L. album* nectary height was reported by Gulyás [1967] to be 730 μm , which granted it the fourth place among the 8 *Lamium* species investigated by the author. The author assigned the same place for the species as far as the quantity of secreted nectar was concerned and noted that the larger nectaries of the *Lamium* species produced substantially greater amounts of nectar than small ones. Similar relationships between the nectary size and nectar abundance in closely related Lamiaceae plants were reported by Dafni et al. [1988] and Kertesiz [1996].

The content of sugars in the *L. album* nectar was 43% and it was almost 10% lower than that described by Jabłoński [1960]. Similar values were reported by Kugler [1970] 42% and Gulyás [1967] 46%, whereas Maurizio and Grafl [1969] showed lower concentrations of sugars for this taxon (29–38%) (tab. 2). The mass of sugar obtained from one flower in the present study is similar to the data provided by Jabłoński [1960], Maurizio and Grafl [1969] and almost twice as higher as that presented by Gulyás [1967] and Bodnarčuk et al. [1993]. Comparison of *L. album* honey yield determined by various authors revealed considerable differences. Our results ($191 \text{ kg} \cdot \text{ha}^{-1}$) belong to the high values and are similar to the yield presented by Jabłoński [1960] and Maurizio and Grafl [1969]. Only Demianowicz [1953] obtained almost a half lower values (tab. 2). Large discrepancies in honey yield may result from the different nectar abundance of individual flowers and the different number of flowers per the unit area [Jabłoński 1986]. The parameters mentioned above are determined by climatic-habitat factors and exhibit the considerable variability in individual years [Jabłoński 1986, Mačukanović-Jocić and Durđević 2005, Jarić et al. 2010].

Our investigations and literature data indicate that *L. album* flowers producing abundant quantities of nectar secrete large amounts of sugars during many weeks of the growing season. They are a valuable source of nectar reward for various representatives of Apoidea, including bumblebees and honeybees.

CONCLUSIONS

1. High contents of sugars in nectar as well as considerable sugar and honey yields of *Lamium album* ensure attractiveness of the flowers of this species to Apoidea and other pollinating insects.

2. Occurrence of pollen presenters on anthers, fragrance attractants and coloured indicators on the *L. album* corolla and stamens are real adaptations for pollination by Apoidea.

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PRZYSTOSOWANIA KWIATÓW *Lamium album* L. DO ZAPYLANIA PRZEZ APOIDEA

Streszczenie. Obecność roślinności ruderalnej oraz śródpolnej sprzyja zachowaniu bioróżnorodności oraz stanowi dodatkowe źródło pokarmu dla owadów zapylających. *Lamium album* należy do pospolitych roślin ruderalnych i jest chętnie oblatywana przez różne grupy owadów, dostarczając im pyłku i nektaru. W latach 2012–2013, na terenie miasta Lublina (Polska) analizowano atraktanty sygnalizacyjne oraz pokarmowe w kwiatach *L. album*, wykorzystując mikroskopię świetlną i skaningową elektronową. Przy zastosowaniu metody pipetowej określono obfitość nektarowania kwiatów, a przy użyciu refraktometru Abbego zawartość cukrów w nektarze. Stwierdzono, że kwiaty jasnoty białej emitują zapach i wyposażone są we wskaźniki nektaru, a korona i pręciki posiadają włoski gruczołowe i papille wydzielające olejki eteryczne. Na pręcikach występują także włoski niegruczołowe pełniące funkcję prezenterów pyłkowych. Nektarnik w kwiecie jasnoty białej ma kształt nieregularnego dysku otaczającego częściowo podstawę załączni słupka. Średnia koncentracja cukrów w nektarze wynosiła 43%. Obliczona z 1 ha wydajność cukrowa osiągnęła średnio 153 kg, zaś wydajność miodowa 191 kg.

Słowa kluczowe: jasnota biała, nektarnik i nektar, włoski, prezenter pyłkowy, wydajność cukrowa

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