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ORIGINAL RESEARCH PAPER

Flowering, nectar secretion, and structure of the nectary in the flowers of *Acer pseudoplatanus* L.

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Abstract

Flowering and nectar release in *Acer pseudoplatanus* were investigated between 2011 and 2013. The micromorphology of the floral and nectary elements was observed using a scanning electron microscope and the anatomy of nectaries was examined by light microscopy. The inflorescence of the sycamore was found to contain flowers, which were functionally male or functionally female. The life-span of the former was on average 5 days, whereas the latter lived on average 4 days. Both types of *A. pseudoplatanus* flowers had yellow-green nectaries with a similar structure. The nectary tissue formed an elliptical or circular layer located on the receptacle surface between the petals and the pistil. The filament bases were located within the nectary recesses but were not fused with this organ. The nectary margins were slightly undulated. The outer diameter of the nectary was in 3.0–3.25 mm and the thickness of the nectary tissue was in the range of 532–1,023 μm. The nectary of the sycamore flower comprised a single layer of epidermal cells and several layers of secretory parenchyma cells. The average depth of epidermal cells was 16.8 μm. The stomata, which were involved in the secretion process, were arranged unevenly on the nectary surface and were surrounded by six–eight epidermal cells. Visible droplets of nectar accumulated on the nectary surface and thus they were easily accessible to insects. The average weight of nectar from 10 flowers was 16.54 mg (range: 11.0–23.75 mg) and the content of sugars in the nectar was found to be in the range of 23.5–50%, with an average of 37.3%. The calculated weight of sugars in the nectar from 10 flowers was on average 6.11 mg and so the average sugar yield from one sycamore tree was estimated to be 0.65 kg.

Keywords

sycamore; flower micromorphology; nectar production; micromorphology and anatomy of nectary

Introduction

The sycamore (*Acer pseudoplatanus* L.) grows in the mountains of Central, Southern and Southeastern Europe. It occupies habitats in mountain mixed forests. The tree is often planted in parks, gardens, forest tree stands, and along roads [1]. In Poland, the sycamore reaches the northeastern limit of its distributional range and is one of the characteristic trees of the lower forest zone. It requires fertile and moderately moist soils and is very resistant to strong winds [2,3]. In urban conditions, broadleaved trees create mild thermal conditions, reduce pollution and noise [4–6]. The shade cast by the *A. saccharum* Marshall crown has been shown to produce 80% lower irradiance and lower air temperatures [7]. The flowers of many species from the genus *Acer* are an important source of nectar and pollen available for insects [8–10]. It was found that *A. pseudoplatanus* inflorescences are visited not only by honeybees, bumblebees, and solitary bees, but also by dipterans [11,12].

Acer pseudoplatanus is included in the European phenology database, where the dates of "first flower opening" are recorded. This has been the subject of phenological investigations in the Czech Republic, Switzerland, and the United Kingdom, where dates of the different phases of foliage development and flowering of this species have been recorded [13]. The sycamore tree can reach 30–40 m in height [9]. After 20–30 years, the trees bloom for 2–3 weeks in May following the development of leaves [8,14]. The flowers are clustered in 5–15-cm long pendulous racemose panicles. There are 7–10 mm diam. flowers of both sexes in the same inflorescence. Female flowers dominate in the cultivated forms, whereas male flowers are more frequent in wild forms [14]. The yellow-green perianth is pentamerous and choripetalous (= polypetalous) [1]. The flowers are classified as entomophilous-ambophilous with the possibility of pollination by insects or wind, which is associated with the moderate amount of pollenkitt and moderate viscosity of the pollen grains [15]. The highly tomentose ovary is bilocular and the style terminates in a bipartite stigma. The flowers usually have eight stamens [16]. A fleshy nectary located on the receptacle surrounds the ovary and androecium [8,17]. It has an external diameter of 3 mm [9]. Numerous droplets of nectar accumulate on the surface of the nectary disk and are thus available to all insects. The nectar contains three sugars: sucrose, fructose, and glucose, with a significant predominance of sucrose [10]. Sycamore flowers emit a characteristic aroma associated with the presence of amines. Since sycamore flowering coincides with colonization of trees by aphids, bees collect not only nectar from the flowers but also the honeydew deposited on pedicels [14]. Sycamore honeys originate mostly from foothill areas. They are light yellow in color and have a mild flavor and aroma. When crystallized, they have a form of a fine-granular paste [14].

Since there is little information in the literature on the abundance of flowering, the structure of nectaries and secretion of nectar in the sycamore, this research has been undertaken to determine the number of flowers in the inflorescence, the morphology of nectary glands, and the abundance of nectar secreted by the flowers of this species. The sycamore flowering dates were also determined during the 3 study years.

Material and methods

The research was carried out over the years 2011–2013. Plants of *A. pseudoplatanus* growing in the Kalina District in Lublin, Poland were the study material. Flowers and nectaries were measured in fresh flowers and photographed with a stereoscopic microscope coupled to a Nikon Coolpix 4500 camera. The anatomical traits of the nectaries were determined using a Nikon Eclipse 400 light microscope in hand-cut sections from fresh material. The height (to the highest position), the external diameter of the nectaries (n = 20), and the depths of epidermal and parenchyma cells (n = 10) were measured. The micromorphology of floral elements was examined using a scanning electron microscope (SEM). Fragments of flowers and dissected nectaries were fixed in 4% glutaraldehyde in 0.1 M phosphate buffer at pH 7.0 and 4°C. After dehydration in ethanol and in an acetone series, the plant samples were critical-point dried in liquid CO_2 and sputter-coated with gold. The observations and photographic documentation were made using a Tescan Vega II LMU SEM.

In 2012–2013, the abundance of flowering and nectar secretion by sycamore flowers were assessed and the flower life-spans determined. Nectar secretion was evaluated with the pipette method [18]. In total, 18 samples were collected; one sample contained nectar produced by 10–60 flowers. Nectar was collected throughout the flower life-span. The percentage of sugars in the nectar was determined using an Abbe refractometer. The average weight of sugars secreted by 10 flowers in the nectar was calculated. The sugar yield was calculated based on the average weight of sugars in the nectar and the flowering abundance. The number of flowers was estimated on randomly selected trees (n = 6). The number of boughs on the trees was determined and first-order branches were counted on selected boughs (n = 6). The inflorescences on the branches were then counted and the number of functionally male and female flowers in the inflorescences (n = 18) of the examined trees was assessed. The length of flowering of the sycamore was determined based on observations of selected trees (n = 6).

Data on nectar weight as well as the concentration and weight of sugars secreted in the nectar were subjected to two-way analysis of variance. The significance of any differences between the means was determined using the Tukey's test at the assumed significance level of $\alpha = 0.05$. STATISTICA ver. 6.0 was used for the calculations.

Results

Structure of *A. pseudoplatanus* inflorescences and flowers

Sycamore flowers formed a panicle (Fig. 1A,B). In each inflorescence, there were both functionally male flowers with long stamens and a variously reduced pistil (Fig. 1C,D) and functionally female flowers with a large pistil and short stamens producing pollen retained in the anthers (Fig. 1E–G). On average, there were 79 functionally male flowers and 30 female flowers per inflorescence. Depending on the location in the inflorescence, the diameter of the flowers was in the range of 8–11 mm. The unattractive pentamerous green perianth was composed of two whorls. The sepals were on average 3.7 mm long and 1.1 mm wide and the petals were slightly shorter (3.0 mm) and much narrower (0.6 mm). The lower part of the adaxial surface of the sepals exhibited viable unicellular trichomes, which may play an important role in withholding the nectar inside the flower (Fig. 1D,F). The epidermal cells on both perianth surfaces displayed cuticular striae (Fig. 1H).

The androecium was formed of eight stamens arranged in one whorl. The filaments were attached to recesses visible on the nectary disk surface (Fig. 1F, Fig. 2A,B). The surface of the large, flattened ovary of functionally female flowers was covered by long, viable, unicellular trichomes. The hairless style had a bipartite stigma (Fig. 1I–K) and the surface of the stigma was covered by densely arranged papillae (Fig. 1J,K).

Flowering length and abundance

The sycamore trees studied began to flower on similar dates: April 28 in 2011, May 2 in 2012, and April 30 in 2013. The flowering phase ended on May 26 (2011), 29 (2012), and 30 (2013). In all years, flowering persisted from the third decade of April to the third decade of May. The life-span of the functionally male flowers was on average 5 days from the opening of sepals and petals and the functionally female flowers lived shorter, an average of 4 days.

The average number of branches on a single tree in the study years was 10.3 and the average number of inflorescences on a single branch was calculated. The greatest number of inflorescences was recorded in 2012 (1,088); the values in 2011 (869) and 2013 (895) were similar. There were on average 108 flowers in the sycamore inflorescence and the average number of flowers on a tree was calculated to be 1,059,620 (Tab. 1).

Structure of the nectary

The *A. pseudoplatanus* flowers examined had yellow-green nectaries with a similar structure in flowers of both sexes (Fig. 2A,B). The nectary tissue constituted a fleshy elliptical or circular layer located on the receptacle surface between the petals and the pistil. The filament bases were located within the recesses visible on the nectary but were not fused with this organ (Fig. 2A–C,F,I). The nectary margins were slightly undulated. The nectary in the buds of functionally female flowers was green (Fig. 2G) but turned yellow at the pistil maturity phase (Fig. 2H) and in male flowers in the full bloom phase (Fig. 2J).

The outer diameter of the nectary was found to be 3.0–3.25 mm. The thickness of the nectary tissue was in the range of 532–1,023 μm and that of the secretory tissue in the two types of flowers was similar: 734.5 μm in the functionally female flowers and 776.5 μm in the male flowers. The sycamore nectary was composed of an uniseriate epidermis and several layers of secretory parenchyma cells. The average depths

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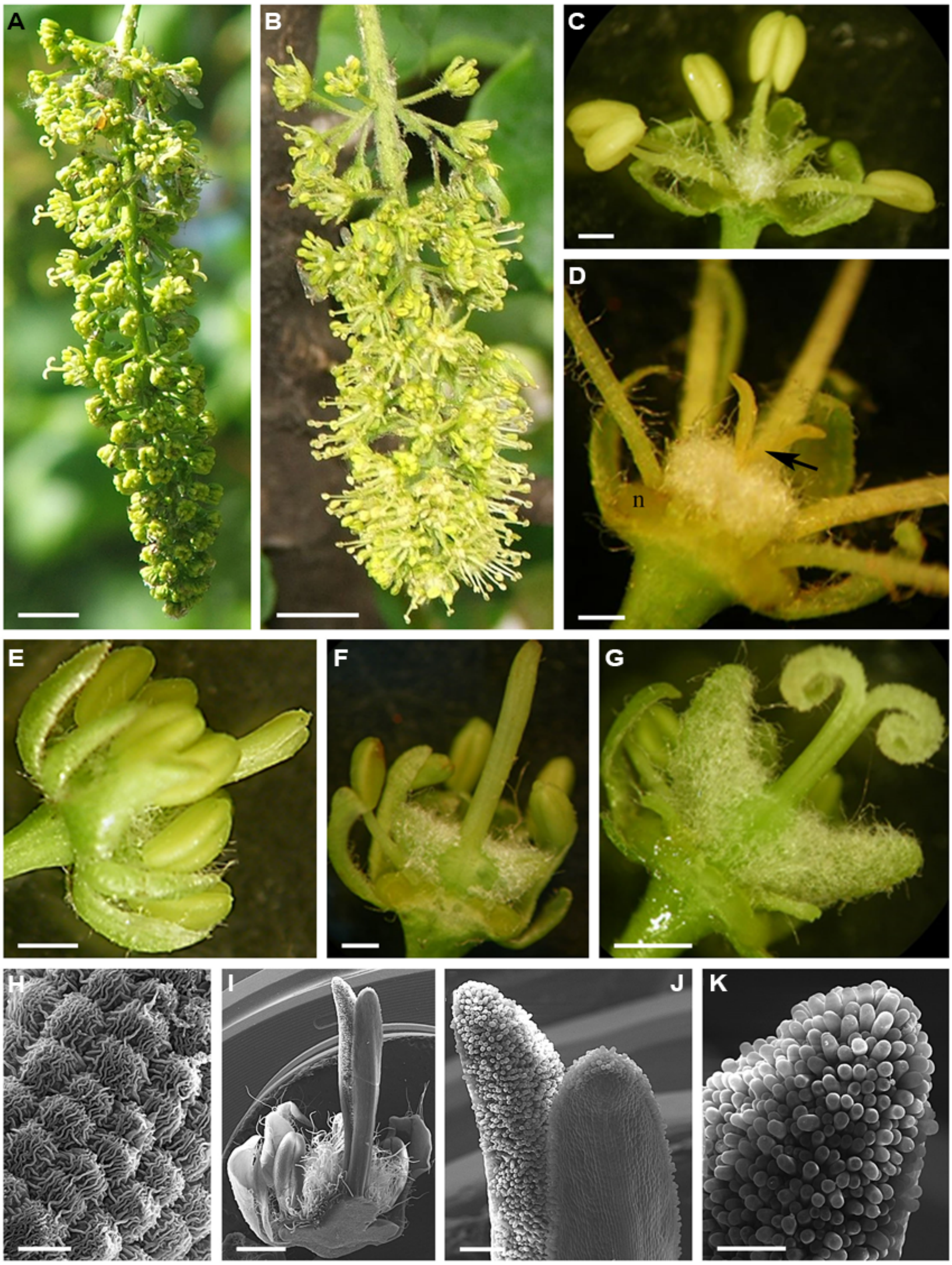

Fig. 1 *Acer pseudoplatanus* inflorescences, flowers, and floral elements. (**A**) Young inflorescence with visible functionally female flowers; bar = 2 cm. (**B**) Inflorescence with visible functionally male flowers; bar = 2 cm. (**C,D**) Functionally male flowers; bar = 2 mm: absence of a pistil (**C**), reduced pistil, absence of a style, sessile stigma (arrow) (**D**). (**E–G**) Functionally female flowers in various stages of development; bar 2 mm. (**H**) Fragment of epidermis in corolla petals, striae on the epidermis; bar = 20 µm. (**I–K**) Stigma in functionally female flowers; bars: 1 mm (**I**), 100 µm (**K**), 200 µm (**J**). n – nectary.

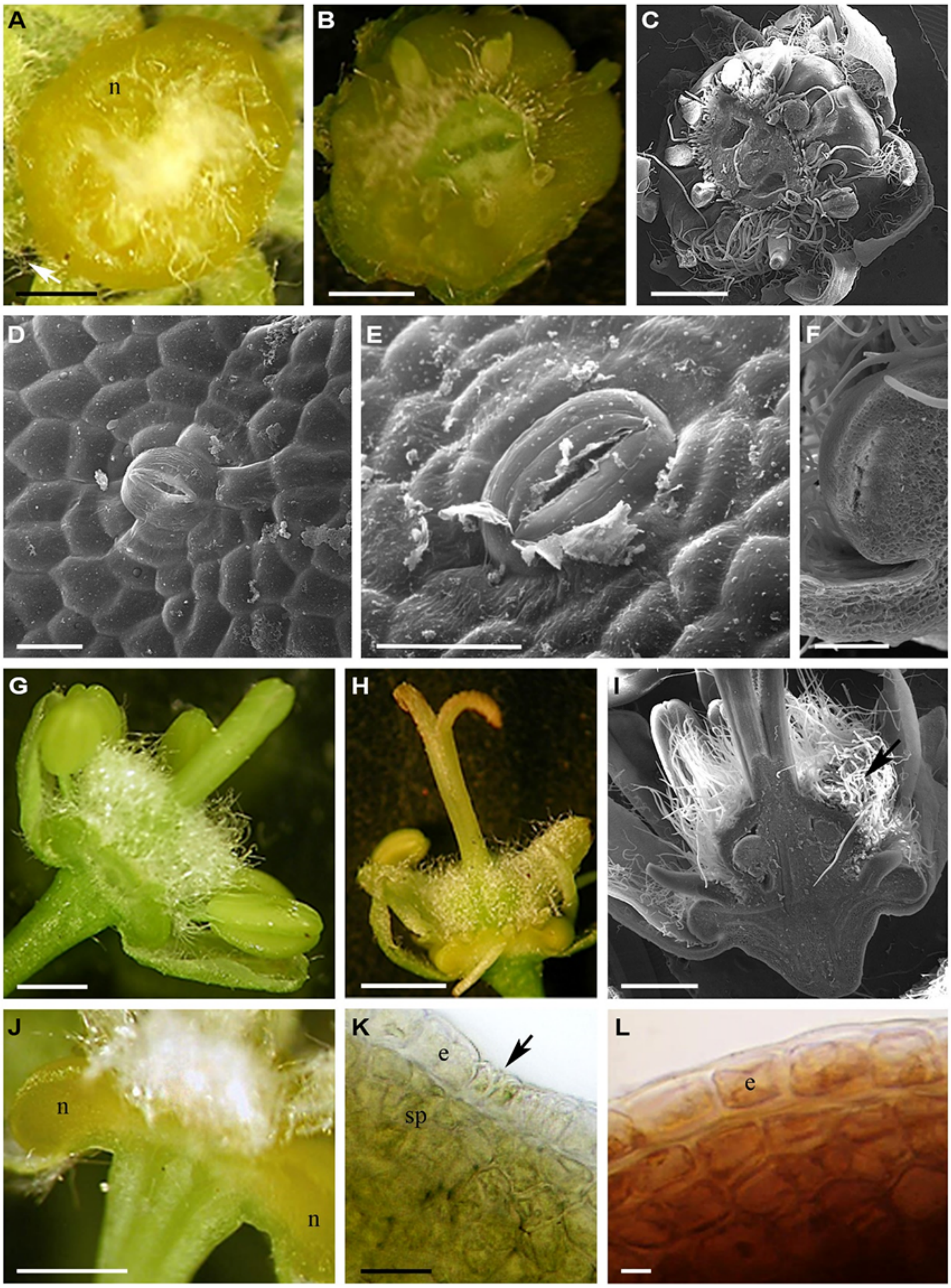

Fig. 2 Fragments of *Acer pseudoplatanus* flowers with a nectary. (**A**) Nectar layer on the nectary surface, trichomes on the perianth (arrow). (**B**) Top view of the nectary after removal of the stamens and perianth. (**C**) Nectary surface with recesses at the stamens; bar = 1 mm (**A–C**). (**D,E**) Nectary stomata: before the nectar secretion phase (**D**) (bar = 50 µm), during nectar secretion (**E**) (bar = 20 µm). (**F**) Nectary margin in the longitudinal section; bar = 200 µm. (**G**) Green nectary in the bud of a functionally female flower; bar = 2 mm. (**H**) Orange nectary in the stage of the pistil receptivity phase in a functionally female flower; bar = 2 mm. (**I**) Vertical section of a flower with a visible nectary and trichomes on the ovary; bar = 1 mm. (**J**) Yellow-green nectary in the longitudinal section in a functionally male flower; bar = 0.5 mm. (**K**) Longitudinal section of the nectary in a functionally female flower in the bud phase, stomata (arrow); bar = 60 µm. (**L**) Longitudinal section of the nectary in the pistil receptivity phase, visible cell walls of the epidermis and subepidermal parenchyma; bar = 10 µm. n – nectary; e – epidermal cells; sp – subepidermal cells.

Tab. 1 Abundance of flowering of *Acer pseudoplatanus* in the years 2011–2013.

Year	Number of flowers on the inflorescence	Number of inflorescences on the tree	Number of flowers on the tree
2011	109.00	8,981.00	978,929.00
2012	106.50	11,236.32	1,196,668.00
2013	108.50	9,246.66	1,003,262.60
Mean	108.00	9,821.33	1,059,619.80

Tab. 2 Amount of nectar, sugar content of nectar, and total sugar mass in nectar per 10 flowers of *Acer pseudoplatanus* in 2011–2013.

Year	Nectar amount (mg)	Sugars content in nectar (%)	Weight of sugars in nectar (mg)
2011	14.54 [a]	39.83 [a]	5.73 [a]
2012	15.87 [a]	37.50 [a]	6.01 [a]
2013	18.27 [a]	34.67 [a]	6.48 [a]
Mean	16.23	37.33	6.10

Values are means ±*SD*. Means in columns with the same letters are not significantly different at α = 0.05; the HSD Tukey test was used.

of epidermal cells was 16.8 µm. The measurements of the parenchyma cell diameter showed that the subepidermal cells were smaller (15.61 µm) than the cells in the middle layer (18.07 µm).

Intense nectar secretion was observed in the stage of pistil and stamen maturity. The stomata involved in this process were elevated above the other epidermal cells. They were arranged unevenly on the nectary surface and were surrounded by six–eight epidermal cells (Fig. 2D,E). Residues of secreted nectar around the stomata were observed using SEM (Fig. 2E). The cells in the nectary observed in the bud phase were smaller (Fig. 2K) than in the nectary sampled in the full bloom phase (Fig. 2L). The vertical section of the nectary demonstrated large, flattened epidermal cells with slightly convex external walls. The walls of these cells were thin and covered with a smooth cuticle layer. A characteristic trait of the epidermis and subepidermal parenchyma cells was the significant thickness of their periclinal walls (Fig. 2L).

Nectar secretion in the sycamore

Visible droplets of nectar were found to accumulate on the nectary surface and were thus easily accessible to insects. Numerous bees were noted visiting the flowers of the trees studied. The average weight of nectar from 10 flowers was 16.54 mg (range: 11.0–23.75 mg). The content of sugars in the nectar ranged from 23.5% to 50%, with an average of 37.3%. Thus the weight of sugars in the nectar from 10 flowers could be calculated; it reached an average 6.11 mg (Tab. 2). The calculated average sugar yield from one sycamore tree was 0.65 kg. The lowest sugar yield was recorded in 2011 (0.56 kg) and the highest value in 2012 (0.73 kg) (Fig. 3).

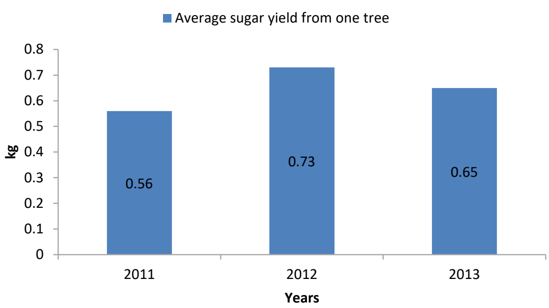

Fig. 3 Sugars yield of *Acer pseudoplatanus* in the years 2011–2013.

Discussion

Two types of flowers were distinguished in the *A. pseudoplatanus* inflorescences examined: (*i*) functionally male flowers with long stamens producing fertile pollen and sterile pistils and (***ii***) functionally female flowers with a large pistil and short stamens producing pollen retained in the anthers. Other authors describe similar types of flowers in inflorescences of *A. pseudoplatanus* [19,20], *A. platanoides* L. [21,22], and *A. oblongum* Wall. ex DC [23]. Rosando et al. [24] distinguished bisexual and male flowers in *A. ginnala* Maxim. and *A. tataricum* L. Renner et al. [25] underlined the labile sex expression in the flowers of various *Acer* species, which is consistent with our observations of the presence of pistils of various sizes in the functionally male *A. pseudoplatanus* flowers.

The nectaries in the different types of *A. pseudoplatanus* flowers had a similar structure. They should be classified as receptacular interstaminal nectaries due to their location exactly between the stamens [17,26].

This study presents for the first time the micromorphology and anatomy of the *A. pseudoplatanus* nectary, which has not been documented so far. The outer diameter of the nectary reached 3.25 mm, which is similar to the value reported by Lipiński [9]. The thickness of the nectaries examined in the functionally male and female flowers was on average 765 μm, with extreme values in the range of 532–1,023 μm. These data indicate that the nectary is characterized by a greater thickness than the corresponding gland in *A. platanoides* flowers, whose thickness was 400–700 μm [22]. The authors also found that the stomata were evenly distributed in the epidermis of the *A. platanoides* nectary, whereas the present study shows that the stomata in the *A. pseudoplatanus* nectary were arranged irregularly. Data presented by Haragsim [27] indicate that *A. platanoides* has a substantially greater number of stomata per nectary unit area than in *A. pseudoplatanus*.

The observations using SEM showed that the nectar-secreting stomata in *A. pseudoplatanus* were slightly elevated over the other epidermal cells. Similar observations were reported by Weryszko-Chmielewska and Sulborska [22] in the case of *A. platanoides*. Before nectar secretion, the stomata are located in recesses. Elevation of active stomata over other epidermal cells have also been observed in other species [28–30]. Comparison of the nectary cell surface in both *Acer* species viewed in SEM demonstrated that the cuticle in *A. pseudoplatanus* examined in the present study was smooth, whereas cuticle striation was noted in *A. platanoides* [22]. Our observations on the location of the nectary relative to the stamens disagree with the data reported by Lipiński [9]; we have shown that the stamens were located in nectary recesses, likewise in *A. platanoides* [22].

Comparison of the micromorphology of the ovaries in *A. platanoides* [22] and *A. pseudoplatanus* analyzed in the present study revealed differences in the presence of secretory trichomes on the epidermal surface. Only the former species has small several-celled capitate trichomes, whereas the latter species has long, viable, unicellular trichomes.

Although all insect-pollinated *Acer* species secrete nectar abundantly, many authors claim that the sycamore plays the most important role as a source of spring reward [14,27]. As shown in the present study, the weight of nectar secreted throughout the life-span of sycamore flowers differed between the years in the range of 1.45–1.82 mg. The average weight of nectar collected from one flower was 1.62 mg. Haragsim [27] demonstrated that one flower of this species produced 0.98 mg of nectar per day, and half the amount was recorded in the case of *A. platanoides*. Contrasting findings were reported by Lipiński [9], i.e., *A. pseudoplatanus* has no such melliferous potential as *A. platanoides*; yet, it plays a significant role as spring reward, as it flowers later and longer during a stable weather period when the number of flying bees in bee colonies increases. Pritsch [8] assessed nectar production on a 4-point scale as very good (4) in the case of the sycamore, and as less abundant in the case of the Norway maple (3). As established by Maurizio and Grafl [14], the average weight of nectar secreted by an *A. platanoides* flower is 0.95 mg per day. The results of the present investigations on the weight of sugars produced by one flower are similar to those reported by Somme et al. [10], i.e., 0.61 mg and 0.67 mg, respectively. These authors [10] reported that *A. pseudoplatanus* nectar was dominated by sucrose. They showed that *A. pseudoplatanus* ranked third out of nine entomophilic tree species from the urban greenery of Brussels in terms of the content of nectar sugars, after *Robinia pseudoacacia* L. (1.28 mg) and *Tilia ×euchlora* Koch (0.96 mg). Therefore, the species examined in the present study can be recommended for planting in urban greenery.

Climate changes related to global warming recorded in recent decades have influenced plant development, including flowering (e.g., [31–37]). In our investigations, the flowering period of *A. pseudoplatanus* was found to increase by 3 days in 2013 (32 days) compared to 2011 and 2012 (29 days). Juknys et al. [38] showed that the growing season of *A. platanoides* increased by 25.4 days in 1956–2009. Similarly, based on 65-year phenological studies, Kolarova et al. [39] reported significant extension of the growing season of *A. platanoides* and *A. pseudoplatanus* in the Czech Republic. A 15-year study conducted by Weryszko-Chmielewska et al. [16] demonstrated acceleration of flowering of various *Acer* species, which was evidenced by records of airborne pollen of this taxon. In their aerobiological studies, these authors also found increased pollen production by trees from the genus *Acer* during the study period. It can be assumed that climate warming does influence the amount of nectar produced by flowers.

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Kwitnienie, nektarowanie i budowa nektarnika w kwiatach *Acer pseudoplatanus* L.

Streszczenie

W latach 2011–2013 prowadzono badania dotyczące kwitnienia i nektarowania *Acer pseudoplatanus*. Mikromorfologię elementów kwiatu i nektarnika określono przy użyciu skaningowego mikroskopu elektronowego. Anatomię nektarników zbadano metodami mikroskopii świetlnej. W kwiatostanie klonu jaworu stwierdzono średnio 108 kwiatów. Wyróżniono kwiaty funkcjonalnie męskie i funkcjonalnie żeńskie. Długość życia kwiatów funkcjonalnie męskich wynosiła średnio 5 dni, a funkcjonalnie żeńskich średnio 4 dni. W obu typach kwiatów występują żółto-zielone nektarniki o podobnej budowie. Tkanka nektarnikowa ma postać eliptycznej lub kolistej warstwy położonej na powierzchni dna kwiatowego między płatkami a słupkiem. Nasady nitek pręcikowych znajdują się w obrębie zagłębień nektarnika, ale nie zrastają się z nim. Brzegi nektarnika są lekko pofałdowane. Średnica zewnętrzna nektarnika wynosi 3,0–3,25 mm. Grubość tkanki nektarnikowej zawarta jest w przedziale 532–1023 µm. Nektarnik klonu jaworu zbudowany jest z pojedynczej warstwy komórek epidermy i kilkunastu warstw komórek parenchymy wydzielniczej. Średnia wysokość komórek epidermy wynosi 16,8 µm. Aparaty szparkowe uczestniczące w procesie sekrecji rozmieszczone są nierównomiernie na powierzchni nektarnika. Otoczone są przez 6–8 komórek epidermy. Nektar zbiera się w postaci widocznych kropli na powierzchni nektarnika i jest łatwo dostępny dla owadów. Średnia masa nektaru z 10 kwiatów wynosiła 16,54 mg (zakres 11,0–23,75 mg). Zawartość cukrów w nektarze wahała się w granicach 23,5–50,0%, średnio 37,3% Wyliczono masę cukrów w nektarze z 10 kwiatów, która osiągnęła średnio 6,11 mg oraz średnią wydajność cukrową z pojedynczego drzewa klonu jaworu, która wynosiła 0,65 kg.