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DIURNAL AND SEASONAL DYNAMICS OF NECTAR SECRETION OF SOME SPECIES IN THE FAMILY LAMIACEAE

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Results obtained during evaluation of diurnal and seasonal variations of nectar secretion of Ballota nigra, Prunella vulgaris and Lamium album during the period from June to September, 1997 in the region of Belgrade showed that nectar production is a complex physiological process variable due to species-specific characteristics and depending to a great extent upon the environment conditions present in habitats.

Nectar secretion increased from morning to afternoon when conditions for plant development were optimal (sunny, warm, rainless and windless weather) while a decrease in relative air humidity allowed maximal nectar secretion between 12 and 2 p. m. in all monitored plants. Nectar secretion decreased during the afternoon, after the peak was achieved. Nectar production decreased in cloudy rainy and windy weather, due to a poor combination of microclimatic conditions in the habitats, especially low temperature, high relative humidity and low insolation, during August in all three species.

Comparative analyses of nectar secretion in B. nigra growing in two environmentally different habitats did not reveal a close relationship between nectar production and environmental changes except for more intensive nectar secretion in a sunny habitat, with a higher temperature.

Dependence of nectar secretion on the period of anthesis was established, since plants secreted more nectar at the beginning and during massive flower formation (June-August) than at the end of the anthesis (September). Exceptionally, nectar secretion of B. nigra, which has a longer flowering period lasting until the end of October, was continual during the whole season. The highest nectar production per day and per flower was estimated in Prunella vulgaris, while L. album showed the lowest production among the monitored plants.

Key words: nectar, nectar production, melliferous plant

INTRODUCTION

Results obtained during evaluation of the apiflora inhabiting the meadow phytocoenosis of the forest-steppe region of Belgrade, which is characterised by a moderate continental climate are presented in this paper. During the evaluation diurnal and seasonal variations of nectar secretion were analysed in order to determine the activity of the nectaries in flowers and provide a realistic estimation of the nectary potential in three melliferous plants.

The fact that nectar secretion and sugar concentration in nectar are a plant species characteristic which is influenced by environmental conditions occuring during the blooming season is well established. Due to the role of nectar in pollination, it is secreted mainly during the phenophase of the anthesis and relies, among other factors, upon the stage of flower development (Skenderov and Ivanov, 1986). The difference in duration of the anthesis and period of sequential flower formation characterises the species of melliferous plant. Three melliferous plant species: *Ballota nigra, Prunella vulgaris* and *Lamium album*, with long blooming seasons have been targeted in our evaluation. Floral nectaries of these plants are placed by the ovarian base, which is characteristic of most plants in the family Lamiaceae (Fahn, 1979). The position of the floral nectaries of these species allows protection from fast evaporation and avoids rinsing nectar away by rain. At the same time it represents an adaptation of the flowers to entomophilia.

The aim of the evaluation was to explore the influence of environmental conditions, especially climatic factors, occuring during the day and season on nectar production in three plant species growing in the same habitat. Diurnal and seasonal dynamics of nectar production in different populations of the same plant species have also been evaluated.

MATERIAL AND METHODS

Nectar samples were obtained from the flowers of Ballota nigra, Lamium album and Prunella vulgaris (Lamiaceae) during the vegetation period in 1997.

Ballota nigra L. (black horehound) is a plant of Mediterranean and Central European origin growing in habitats in the Mediterranean basin, including West Asia, the Danubian basin and North Africa. It also grows on waysides in shade and on waste places, both in urban areas and natural meadows. Groups of 4-10 flowers form characteristic diffuse dihiasis on short hold with pseudovertebrae at the base of the leaf. Corollas are violet. Flowers develop from June to October. Melliferous characteristics of the plant are excellent attracting bees during the whole day (Jašmak, 1973).

Lamium album L. (White dead-nettle) is a perennial plant inhabiting neglected terrain, hedges, fences, around warehouses and urban areas. White flowers in groups of 6-16 are arranged in whorls on the tips of the stem and stalks. Bees, collections nectar and pollen are well attracted by the plant (Lazarov et al., 1971).

Prunella vulgaris L. (Seff-heal) is a perennial of cosopolitan character, growing in Europe, Asia, Australia, North Africa, and North America. In Serbia it inhabits meadows, pastures, fallow fields, midwood meadows and roadsideverges. It is a member of a large number of plant associations, mostly growing in mesophylic habitats. Dark violet flowers developing from June to September, are arranged in whorls of 4-6 placed above the last pair of leaves, forming the pseudospikes on the tips of the stems.

Nectar was collected from plants growing in meadows around Bojčinska Forest, Srem (30 km from Belgrade). Samples of *Ballota nigra* were collected from two localities differing in environmental conditions. The first (I) locality is insolated during the whole day and plants of the three species grow close to each other. The second locality (II) about 30 m away from the first is shaded during the day, without direct sun.

The intensity of nectar secretion was established directly by the method of Kuliev (1951), based upon capillary flow of the nectar from the flower.

Sampling was performed monthly from June to September, at two hour intervals from 8 a. m. to 6 p. m.

Three to five plants of each species were randomly chosen for daily sampling. Inflorescences of the chosen plants were covered by cotton gauze or plastic wrapping in case of rain and to prevent visits of pollinator insects.

A microcappillary glass tube, 0,3 mm was used to obtain nectar from ten flowers, while the column was measured on millimetre paper. The volume of collected nectar was calculated from:

$V (mm^3) = r^2 \Pi \, . \, H$

r - radius of the capillary glass tube (mm^2)

H - height of the nectar in the tube (mm)

During collection of the nectar, relative air humidity (%) and air temperature (^0C) were estimated in both localities.

Percent sugar concentration in nectar was estimated by field refractometar.

RESULTS

The diurnal and seasonal dynamics of nectar secretion in the three plants is presented in figures 2 and 4, while parameters of the microclimate (air humidity and temperature) are shown in Figures 1 and 3. Total daily nectar production (from 8 a. m. to 6 p. m.) in June, August and September is presented in Figure 5.

The period of early sumer, 1997 was characteristically warm and sunny without wind and rain. Environmental mycroclimatic parameters in the first habitat (Locality I) on 27^{th} June showed a gradual temperature increase from morning to afternoon. The daily maximum (28,6^{0}C) was obtained at 2 p. m., followed by a decrease of the temperature towards the evening (Figure 1a).

The highest relative humidity was at 8 a. m. (80%) qradually decreasing during the day. At 6 p.m. half of the morning value was observed. The wather was sunny without rain 1.

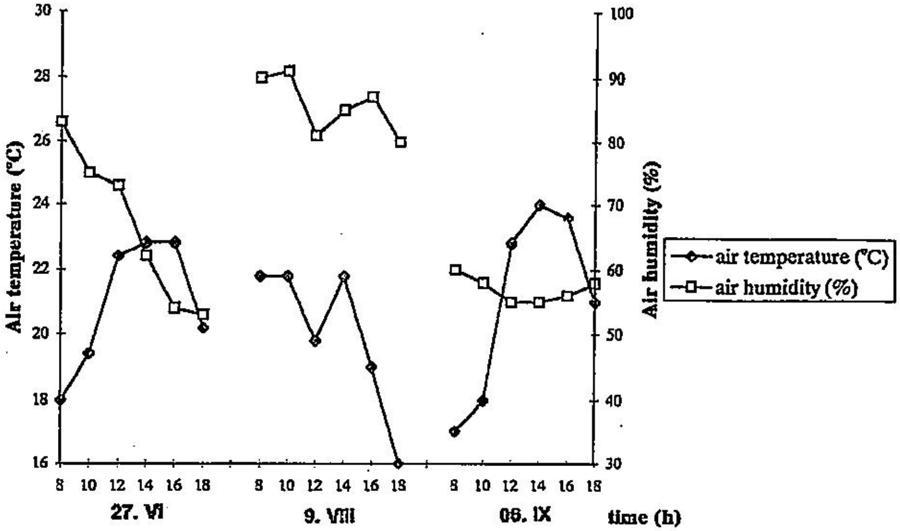

Figure 1. Diurnal and seasonal changes in air temperature and air humidity at locality I

Periodical collection of the nectar revealed increased production during the day, with the peak between 12 and 2 p. m. in all three plant species (Figure 2),

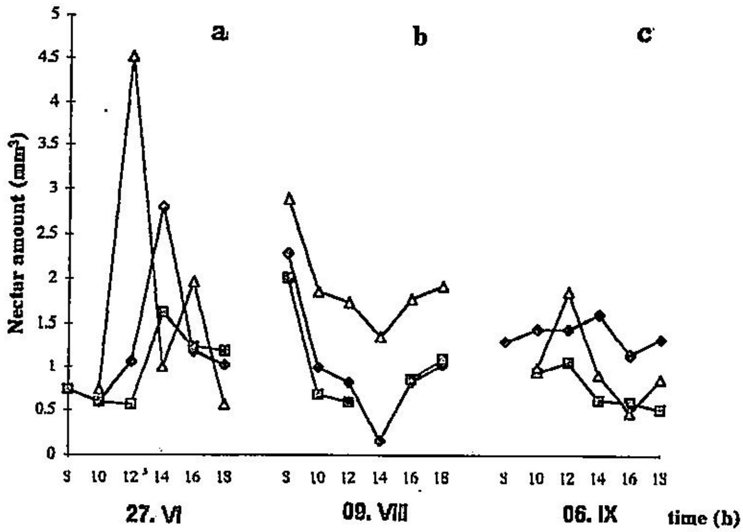

Figure 2. Diurnal and seasonal dynamics of nectar secretion of the species Ballota nigra, Lamium album and Prunella vulgaris at locality I

Nectar production of Prunella vulgaris was the highest both for estimated daily maximum (noon to 2 p. m. value: 4,514), and total daily volume (8,776 mm^3). Each collection attempt succeeded, as some nectar was obtained at each sampling, which did not occur in the other two plants. Lamium album especially had a characteristically low nectar production per flower which resulted in lack of nectar in up to 50% of the flowers, at some sampling intervals. The daily maximum of nectar production by *Ballota nigra* occurred at 2 p. m. (2.803 mm^3) with a total daily volume of 6.668 mm^3.

July and August, 1997, were unusually characterised with low average and maximal daily temperatures. Non-typical climatic conditions were reflected in numerous rainy and cloudy days. The expected dry period of mid-summer was followed with rain in August, all influencing the microclimate in habitat I (Figure 1b). On August 9th, when the second measurement occurred, whole day clouds produced rain in the afternoon at intervals. The showers were mild. Conditions gave rise to high levels of relative humidity at locality I (83-91%), with the daily maximum at8 a. m. followed by a slight decreasing trend during the day. The temperature was lower than the average for August and ranged from 18-22. 6°C, fluctuating but remaining in narrow limits the whole day. The dynamics of nectar production as influenced by the environmental conditions was completely opposite to the results obtained in June. Nectar production was low compared to June, with a continual decreasing tendency towards the evening in all three species. (Figure 2b). The daily peak collection was at 8 a. m., when 2.891 mm^3, 2.006 mm3, nector secretion of *B. nigra* was approximately one-hakf 6,108 mm^3, and 2.272 mm^3 of nectar were collected from the flowers of P. *vulgaris, L. album* and *B. nigra,* respectively.

The highest nectar production occurred in flowers of *P. vulgaris*, with a total daily volume of 11.536 mm^3, nectar secretion of B. nigra was approximately one-half 6.108 mm^3 while the lowest production was evident in *L. album* with only 5.223 mm^3 per day.

Nectar production of the same species during the late summer was evaluated on September 6 th. The daily temperature ranged from 18-27.6°C measured at 8 a.m. and 4 p. m., respectively, while the relative humidity ranged from 58% at 8 a. m. to 47% at 6 p. m. (Figure 1c). The weather was sunny without rain.

The highest nectar production in the occurring conditions, was found in *B. nigra,* with a daily valume of 8.272 mm^3. This species is characterised with the longest flowering period lasting to October. In contrast, the *P. vulgaris* population was rare during September, with a smaller number of flowers per plant. During this period *P. vulgaris* nectar production was diminished (total volume per day: 5.105 mm^3), while *L. album* nectar production was even lower compared to the other two species and to values obtained at the previous two measurements (Figure 2c). Although the pattern of nectar secretion resembled that found in June, the number of nectar containing flowers was lower, the quantity of nectar obtained per sampling was lower and total nectar volume per day was smaller compared to the values obtained in June.

Besides evaluation of the daily and seasonal nectar production of the three melliferous plants growing in the same environmental conditions, the nectar secretion of *B. nigra* in two environmentally different habitats was evaluated. Environmental conditions of locality II were modified compared to the conditions present in habitat I. The second locality was in deep shade, since the sun was hidden by treetops during the whole day. Apart from the absence of direct sunlight, plants were exposed to lower temperatures and higher humidity compared to the environment of locality I (Figures 3 and 4).

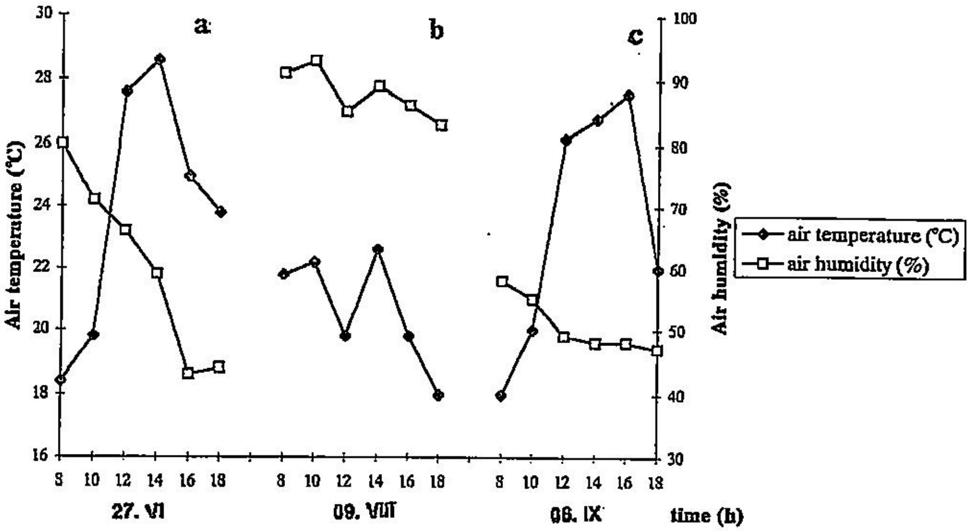

Figure 3. Diurnal and seasonal changes in air temperature and air humidity at locality II

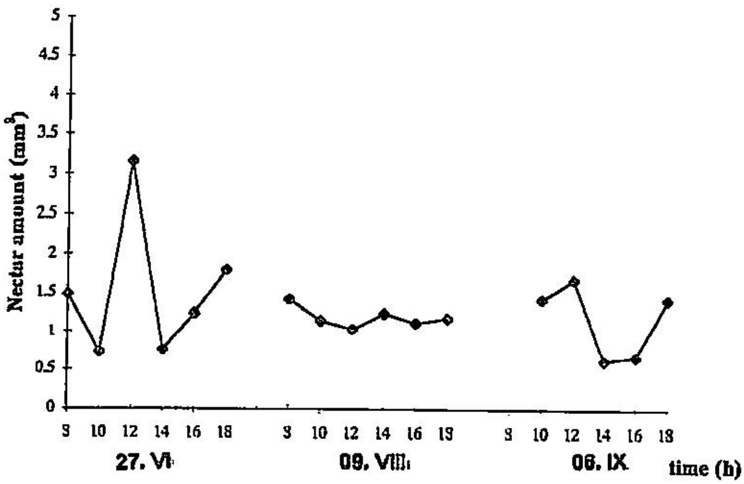

Figure 4. Diurnal and seasonal dynamics of nectar secretion of the species Ballota nigra at locality II

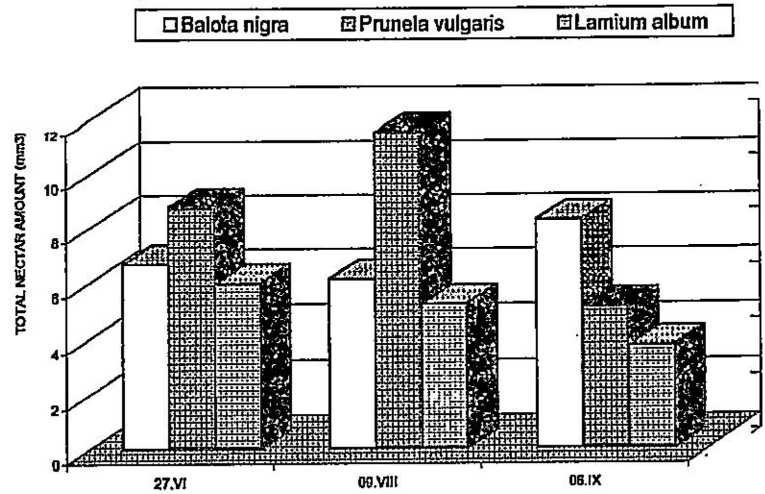

Figure 5. Diurnal and seasonal variations of nectar amount in flowers of Ballota nigra, Prunella vulgaris and Lamium album during the period June-Septeber 1997. at locality I

The sugar concentration, determined at 10 a. m. on June 27 th was 24% in the nectar obtained from *B. nigra* and *L. album,* and 22% in *P. vulgaris.*

DISCUSSION

Nectar production is a physiological process influenced by continual joint effects of numerous endogenous and environmental factors affecting the intensity of secretion.

Internal species-specific factors like flower development, hydration, size and position of the flower, size and position of the nectary, etc. as well as environmental conditions in the habitat influence the quantity and sugar concentration of the nectar. The influence of physiological processes occuring in plants on nectar secretion have been evaluated by many authors (Girnik, 1964; Žukov, 1968; Zauralov, 1966; Kartašova, 1965; Gubarƒ, 1961, etc.) Most of the data refer to changes in nectar production during the ontogenesis of the flower (Ewert, 1940; Fahn, 1949, Feisinger, 1978; Bertin, 1982, McDade and Kinsman, 1980; Southwick and Southwick, 1983; Real and Rathcke, 1991). The most intensive nectar secretion occurs before and during the stage of the fully developed flower, since nectar production is correlated with pollination (Ponomarev and Bannikova, 1960; Mihailova, 1959; Kartašova and Bondarb, 1965; Malahova-Akovleva, 1966). Nectar secretion decreases or stops after fertilization, though in some species, like *Laurus nobilis*, it continues even after fading of the flower (Daumann, 1931). The secretion of nectar appears during the stage of the mature bud just before the corrola opens, lasting during the whole phenophase of the anthesis, in all evaluated species: *L. album, B. nigra* and *P.*

vulgaris. Our exaination revealed nectar secretion in *L. album,* even after partial fading of the corolla leaves, as mentioned by Sernander (1906).

The previously described (Vogel, 1983; Škenderov and Ivanov, 1988; Momirovski and Šimić, 1953; Bernandelo et al. 1990) influence of environmental factors on nectar production was also established. Small variations in temperature, sunlight, humidity of air and soil are reflected in the quantity and composition of secreted nectar.

The evaluation of diurnal dynamics in nectar secretion revealed the extent of environmental influence on nectar secretion in the three Lamiaceae sp. during June, August and September. Nectar secretion occured from morning to afternoon in all three species, and showed similar patterns during the day depending upon the relative air humidity and teperature. Our graphs showing the intensity of secretion and temperature variations, revealed the dominant influence of heat on nectar production as previously described by Škenderov and Ivanov (1986), Momirovski and Šimić (1953) and others. Škenderov and Ivanov stated that the optimal temperature for nectar production varies between 10 and 30°C, while Lazarov et al., (1971) found that optimal temperature levels were 16-25°C, with peaks between 25 and 30°C. Higher teperatures lead to a sudden drop or termination of nectar production. High temperatures leading to drying of nectar did not occur during our evaluation.

Monitoring of daily production in August showed the opposite pattern of nectar production to that during the early and late summer. The decrease of nectar secretion in the middle of the day was induced by unfortunate microclimatic conditions (low temperature, wind, clouds and rain) and probably mostly depressed by high air humidity. Air humidity ranged between 83-93% on 9th August, which is much above the optimal levels of between 60 and 80% for most plants (Lazarov et al., 1971). The change of nectar production due to humidity follows the same pattern in most plants: first an increase of production follows increase of moisture until the peak is achieved, then decreasing production occurs. Periods of moderate rain also influence nectar secretion badly, though Lazarov et al. (1971) described a beneficial effect of rain on nectar production, which depended upon the duration and intensity. Certain researchers pointed out the negative influence of wind, leading to decreased or terminated secretion and evaporation of the water from nectaries, especially in open and uncovered flowers (Lazarov, 1971). Clouds also participated in the decrease of nectar production, since nectar secretion directly depends upon the intensity of photosynthesis, which is sunlight-dependant. This was concluded by Čarnovski (1952) during experiments with darkened bast trees, when photosynthesis stopped, leading to cessation of nectar production in 2-3 days. Reevaluation of the influence of darkness on other plants gave similar results (Girnik, 1958a). Well insolated plants secreted more nectar than darkened ones (Girnik, 1958b).

The complex synergistic effects of environmental factors are presented in Figure 2b where the three curves showing daily secretion of nectar correspond almost idealy.

The visits of pollinator insects to flowers were rare on August 9 th compared to dry sunny days. Comparative analyses of diurnal dynamics of nectar secretion in *B. nigra* inhibiting two environmentally different localities did not reveal a close relationship between nectar production and the different environmental conditions, except for higher intensity of production in locality I, when teperatures were high. Athough the microclimatic condition in the habitats were similar in early and late summer, nectar secrettion was different. Fluctuations in nectar secretion found in locality II in June were irregular, while plants followed similar patterns of nectar production in both localities, in September, but the volumes of nectar per day in locality II were lower in September.

Conditions were similar in both localities during August, leading to similar patterns of nectar production during the day. Sugar concentration, measured once during the vegetative period, was above 20% in nectar of all three plants in June. It is well known that bees preferably collect nectar with 50-56% of sugar (Lazarov, 1971). Different sources have established different diurnal and phenophase dependant patterns of sugar content in nectar. Schemske (1980) noted an increasing pattern, Bertin (1982) did not detect any relationship, while Kakutani et al. (1989) and Steiner (1985) and Steiner (1985) found very variable sugar concentrations due to ageing of the flowers. The values observed here are just informative since sugar content was estimated only once.

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DNEVNA I SEZONSKA DINAMIKA LUČENJA NEKTARA NEKIH VRSTA FAM.LAMIACEAE

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SADRŽAJ

Analiza dnevne i sezonske dinamike nektarske produkcije vrsta Ballota nigra, Prunella vulgaris i Lamium album tokom perioda jun-septembar 1997. godine u okolini Beograda je pokazala da je medenje složen fiziološki proces koji varira shodno specifičnim odlikama svake vrste, a u visokom stepenu je zavistan od ekoloških uslova staništa.

U uslovima optimalnim za razvoj biljaka (vedro, sunčano, toplo, bez kiše i vetra), lučenje nektara se povećava od jutarnjih ka podnevnim satima sa porastom temperature, a smanjenjem rel. vlaž. vazduha, dostiže maksimalnu vrednost između 12 i 14 h kod svih vrsta, a zatim se smanjuje. Opadanje nektarske produkcije po oblačnom, kišovitom i vetrovitom vremenu, je u gotovo idealnim odnosima zabeleženo kod sve tri vrste u avgustu mesecu, a uslovljeno je nepovoljnom kombinacijom mikroklimatskih uslova staništa, pre svega niskom temperaturom, rel. vlažnošću vazduha iznad gornje granice optimalnog i odsustvom sunčevog zračenja.

Komparativnom analizom medenja vrste *Balota nigra* na dva ekološki različita lokaliteta nije bilo moguće utvrditi bližu uslovljenost produkcije nektara promenama u spoljnoj sredini, sem da je medenje bilo nešto intenzivnije na osunčanom staništu pri višoj temperaturi.

Ustanovljena je zavisnost između lučenja nektara i perioda cvetanja biljaka. U početku i u vreme masovnog cvetanja (jun-avgust) biljke luče mnogo više nektara nego pri kraju cvetanja (septembar). Izuzetak je *Ballota nigra,* čiji period cvetanja u uslovima umereno-kontinentalne klime traje do kraja oktobra i kod koje je lučenja nektara ujednačeno tokom čitavog perioda cvetanja.

Od tri analizirane biljne vrste, zapaženo je da se *Prunella vulgaris* ističe najvećom količinom izlučenog nektara po danu, kao i količinom izlučenog nektara po cvetu, a *Lamium album* najnižom.