Acta Botanica Hungarica 45 (3–4), pp. 259–271, 2003

# COMPOSITION OF FLORAL NECTAR AND ITS SEASONAL VARIABILITY IN SOUR CHERRY CULTIVARS

P. BUKOVICS<sup>1</sup>, ZS. OROSZ-KOVÁCS<sup>1</sup>, L. GY. SZABÓ<sup>1</sup>, Á. FARKAS<sup>1</sup> and T. BUBÁN<sup>2</sup>

<sup>1</sup>Department of Botany, University of Pécs, H-7624 Pécs, Ifjúság u. 6, Hungary <sup>2</sup>Research and Extension Centre for Fruitgrowing H-4244 Újfehértó, P.O. Box 38, Hungary, E-mail: silver@ttk.pte.hu

(Received 10 June, 2002)

The sugar composition of floral nectar was studied in 17 sour cherry cultivars in Újfehértó in 1997–2000. All samples contained the three most frequent sugar components: glucose, fructose and sucrose, similarly to our previous data. The ranking of the floral nectar in sour cherry cultivars based on sucrose content was the following: 'Újfehértói fürtös' and 'Pándy 48' reached the threshold value of bee visitation in at least three seasons, and a significant amount of sucrose was detected in the flowers of 'Érdi jubileum AB' and 'Érdi bőtermő' as well. The above cultivars proved to be the most valuable in Újfehértó from the viewpoint of apiculture. According to the ranking based on fructose content, which considers human sensation of taste, the most favourable cultivars were 'Újfehértói fürtös', 'Meteor USA' and 'Korai pipacs'. Based on total sugar content the secretory products preferred by bees were those of 'Újfehértói fürtös' (in three seasons); 'Korai pipacs', 'Érdi nagygyümölcsű', 'Sárándi S/Gy', 'Debreceni bőtermő', 'Kántorjánosi 3', 'Montmorency' and 'Meteor USA' (in two seasons). The ratio of nectar sugars, based on the Baker-quotient, S/(G+F), was sucrose-dominant at least in one season in 'Érdi jubileum AB', 'Érdi nagygyümölcsű' and 'Pándy 48'; hexose-rich in 'Korai pipacs', 'Kántorjánosi 3' and 'Montmorency'; all other cultivars had a sucrose-rich nectar. The nectar of all studied sour cherry cultivars possessed a composition preferred by bees. The basis of bees' nectar preference is the ratio, quantity and concentration of nectar sugar components, which were influenced by the effects of season to a high degree, differing from data in literature. From the viewpoint of nectar composition and concentration the most favourable temperature was around 20 °C.

Key words: floral biology, sour cherry, sugar components of floral nectar

## INTRODUCTION

Among sour cherry (*Cerasus vulgaris* Mill.) cultivars there are more and more autofertile ones, whose pollination often takes place also without any pollen vector. However, foreign pollination can improve quality even in these cultivars. There are also autosterile varieties (*e.g.* the 'Pándy' clones), which remain in cultivation due to their outstanding fruit quality, although their fruit set is not always satisfactory. These cultivars can receive fertilising pollen by the transmission of wind or insects. Thus, if a successful fertilisation should be

0236-6495/\$ 20.00 © 2003 Akadémiai Kiadó, Budapest

achieved even in autosterile sour cherry cultivars, all details of their pollination biology should be known, including the sugar composition of nectar, one of the primary attractants.

It is known from the work of Majer-Bordács *et al.* (1993), dealing with the nectar composition of apricot, that a few percent difference in the refraction of nectar between the pollen donor and the pollinated cultivar may hinder pollen transfer, depending on whether the sugar concentration of the secretory product of the given cultivars reaches the bee visitation threshold.

The majority of our fruit tree cultivars is allogamous (Terpó 1980). Also in the case of allogamy, because of the small likelihood of wind pollination, it is essential to ensure insect pollination with higher certainty of fruit set, the prerequisite of which on the other hand is that sufficient reward is offered by the flower.

The glandular tissue of the nectary plays an important role in concentrating and altering the secretory product. In glands without bundles sugars accumulated in the glandular tissue and nectary parenchyma get into the nectar after a suitable transformation. Thus, the floral secretory product is not primary phloem sap. 31 different sugars were detected in various nectars. From nectar sugars sucrose, glucose and fructose occurred most frequently in plant species. The ratio of these three sugars may change from species to species. The character of nectar and later of honey is also determined by the ratio of the three sugars (Gulyás 1975).

Sugar concentration may be in the range 3–75% in the nectar (Gulyás 1975), and it has to be at least 10% for being collected by bees (Frisch 1950).

The floral nectar of temperate zone fruit trees is a multi-component aqueous solution, whose composition is characteristic for the given plant species or cultivar (Kartasova 1965). Until the 1970s it was believed that energy of nectar as a sugar solution reflects the energy needs of the pollinator. Later other substances than sugars were also found in the secretory product, mainly amino acids, lipids, phosphatases, glycosides, mineral salts, vitamin C and aromatic substances (Maurizio 1960, Baker and Baker 1983*a*, *b*). Baker and Baker (1990) investigated the possible relationship between the chemical composition of nectar and the pollinator animal and found that the quotient sucrose/(glucose+fructose) and the structure of the flower or the inflorescence may refer to the pollinator.

Based on the amount of sucrose and its ratio compared with fructose and glucose, four types of nectar were distinguished:

1. hexose-dominant:	S/(G+F) < 0.1
2. hexose-rich:	S/(G+F) = 0.1-0.49
3. sucrose-rich:	S/(G+F) = 0.5-0.99
4. sucrose-dominant:	S/(G+F) > 1

Large bees prefer the latter two types of nectar, with the prevalence of sucrose.

Orösi (1968) claimed that bees do not taste the nectar sweet if its sucrose content does not reach 4%, or the mixture of glucose and fructose is more dilute than 8–9%.

According to Wykes (1952), Percival (1961) and Kartasova (1965) sugar components and their relative percentage are constant in nectar, their occurrence being characteristic for the given families.

From Rosaceae taxa the nectar composition of fruit tree cultivars was studied by several researchers. Percival (1961) analysed the nectar composition of 43 species in the family. The nectar of all species studied by her contained all three sugars. Sucrose-dominant nectar was found *e.g.* in *Cotoneaster horizontalis* and *Malus sylvestris*. The balanced type of nectar with an almost identical proportion of the three sugars was also found, as *e.g.* in *Prunus domestica*, *P. laurocerasus*, *P. persica*, *P. spinosa*. From the herbaceous Rosaceae the nectar of *Fragaria* was dominated by glucose and fructose in the same ratio, rather than sucrose. Such a proportion corresponds practically to that of honey. Benedek and Nyéki (1997) stated that bee visitation was in strong correlation with the sugar concentration of nectar in the case of flowers of fruit tree cultivars.

Investigating the nectar production and composition of plum cultivars, Simidtschiev (1972) stated that the highest amount of nectar was produced by cv. 'Monfort' and the lowest by cv. 'Blue of Kiustendil'. Refraction of nectar varied between 10–70%. The highest sugar content was found in the nectar of 'Green Gage', the lowest in that of cv. 'Monfort'. In flowers producing nectar abundantly sugar content was lower. 16.66% of the bees collected pollen, 83.34% of them collected nectar and pollen simultaneously. The sugar content of nectar had a great effect on active bee visitation of plum flowers. The flowers of all studied cultivars were actively visited by bees, except for 'Blue of Kiustendil', where the significantly lower bee visitation was due to the small nectar producing capacity.

Majer-Bordács *et al.* (1989) claimed that in the case of plum the secretory product of autofertile cultivars was rich in glucose and poor in sucrose, while that of autosterile ones was richer in sucrose.

Botz *et al.* (2003) found that stone fruit cultivars blooming in early spring are generally characterised by sucrose-poor or sucrose-free nectar, which may be in connection with the dominance of wind pollination and self-fertilisation. Despite of their large nectary, early-blooming almond cultivars produce a dilute, two-component nectar, containing glucose and fructose. The floral secretory product of a single cultivar, 'Tétényi bőtermő' contained a little sucrose, too. At the beginning of blooming, filaments are so rigid and so close to each other that bees are not able to obtain the secretory product, which is not attractive, either. The above fact may explain the apicultural observation that bees hardly visit the flowers in the first three days of blooming. On the second and third day of blooming the nectar accumulating in the flower becomes concentrated to such extent that bees start to collect it. With anther dehiscence filaments lose their rigidity, and bees can reach the nectar through gaps between them.

The nectar of peach cultivars, blooming also early, but slightly later than almond, already contains a small amount of sucrose, therefore, if the secretory product is concentrated enough, it can be very attractive for bees. The prevalence of glucose is characteristic also here, but the concentration of nectar in the majority of the studied cultivars did not reach the threshold value of bee visitation. Since most of the cultivars are self-fertile, insect pollination has a smaller significance (Botz *et al.* 2003).

As described in our previous paper (Orosz-Kovács *et al.* 2000), the floral nectar of sour cherry cultivars is usually attractive for insects, thus for bees as well. Sour cherry orchards offer a sufficient quality and amount of nutritive materials (pollen, nectar) for bees strengthening their families. It was stated that night nectar in sour cherry is more dilute than nectar produced during the day. Sucrose, tasted sweet by bees, is present in more than 30% in the floral nectar along with glucose and fructose. Consequently, for bees the nectar composition of sour cherry cultivars is the most preferred one among stone fruit cultivars.

The aim of the present paper was to further investigate the nectar composition of sour cherry cultivars and determine:

- Apicultural ranking of nectar in sour cherry cultivars based on sucrose content, fructose content (according to human tasting) and total sugar content;
- The ratio of nectar sugars;
- Seasonal differences in nectar composition in sour cherry cultivars;
- Effect of air temperature and precipitation on nectar composition.

#### MATERIAL AND METHODS

Material was collected in the cultivar collection of the Research and Extension Centre for Fruitgrowing, Újfehértó, in years 1997–2000.

The following sour cherry cultivars were examined: 'Újfehértói fürtös', 'Pándy 48', 'Érdi jubileum', 'Meteor USA', 'Montmorency', 'Debreceni bőtermő', 'Nefris', 'Sárándi S/Gy', 'Korai pipacs', 'Mej Djuk', 'Kőrösi korai', 'Érdi nagygyümölcsű', 'Kántorjánosi 3', 'Oblacsinszka', 'Érdi bőtermő', 'Cigány

404'. Examination of each cultivar could not be carried out in all four years due to the weather conditions.

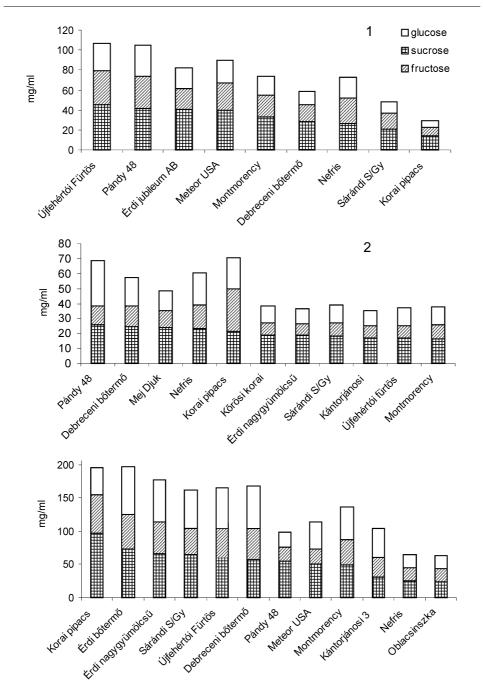
Samples were collected from 20–50 flowers per tree, from 1–3 trees per cultivar. For each sample nectar was extracted with microcapillaries from several pollen shedding flowers having been isolated for 24 hours, and 10  $\mu$ l of nectar was measured into small phials, stored in an exsiccator.

Nectar sugar components were determined by thin layer chromatography, quantitative evaluation was carried out by densitometry (CAMAG TLC Scanner II. at 510 nm wave length). Samples were diluted to 200 µl (20× dilution) in the mixture of ethanol : water 7 : 3. A known amount of the solution was applied to a 20 × 20 silica gel coated plate with microcapillaries. The distance between sample spots was the same, 15 mm being the minimum. The start line was 15 mm from the edge of the plate, the front line 30 mm from the edge. Plates were developed twice without saturation, using ethyl-acetate : ethanol : 60% acetic acid : water saturated with boric acid (50 : 20 : 10 : 10) as developing agent. Plates were dried at room temperature, then treated with a thymolic reagent (0.5 g thymol dissolved in 95 ml ethanol, with 5.0 ml *cc* sulphuric acid) for 3 sec. Finally densitometric evaluation was carried out.

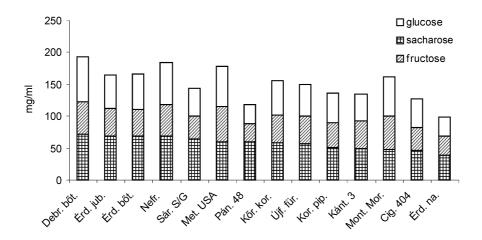
### **RESULTS AND DISCUSSION**

The sugar composition of nectar samples from sour cherry cultivars collected and studied in 1997–2000 is partly similar to our previous data (Orosz-Kovács 1991, Botz *et al.* 2003). The three sugar components found in the greatest amount were glucose, fructose and sucrose in these samples, too. As it is known (see above), for bees the sweetest sugar in nectar is sucrose, being present in more than 30% in the samples, thus sour cherry belongs to fruit tree cultivars with a nectar composition most preferred by bees. However, insect visitation of flowers varies, due to the differences in concentration between cultivars. Flowers with sweeter nectar may have a diverting effect from those with less sweet nectar.

In the ranking based on sucrose content, which, according to literature, is the sweetest and most attractive for bees from the three detected sugar components 'Újfehértói fürtös', 'Pándy 48' and 'Érdi jubileum' reached 40 mg/ml in 1997, which corresponds approximately with 4% refraction, *i.e.* the threshold of bee visitation, thus indicating a nectar surely preferred by bees (Fig. 1). In 1998 none of the cultivars reached this value, sucrose content in the nectar being only 20–30 mg/ml (Fig. 2). In the year 1999 the majority of the cultivars reached or exceeded 40 mg/ml, with the exception of four cultivars (Fig. 3). Similarly to the previous year, the nectar of most cultivars, except for 'Érdi



*Figs* 1–3. Nectar sugar composition of sour cherry cultivars on the basis of sucrose content at Újfehértó: 1 = 1997, 2 = 1998, 3 = 1999



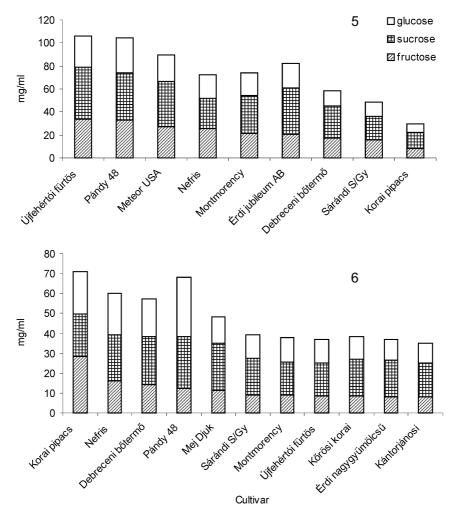
*Fig. 4.* Nectar sugar composition of sour cherry cultivars on the basis of sucrose content at Újfehértó, 2000

nagygyümölcsű', reached 40 mg/ml concentration in 2000 (Fig. 4). Surprisingly, ranking of the cultivars is not the same as in the previous year. For example 'Korai pipacs', being the last one in the 1997 ranking, became the first in 1999. Results depend on blooming stage and ecological factors as well, thus differences in nectar composition may be found within a single season, too. Evaluation of cultivars based on sucrose content is significant because even if nectar concentration does not reach 10%, but sucrose amounts to 4%, bees may still visit the flowers.

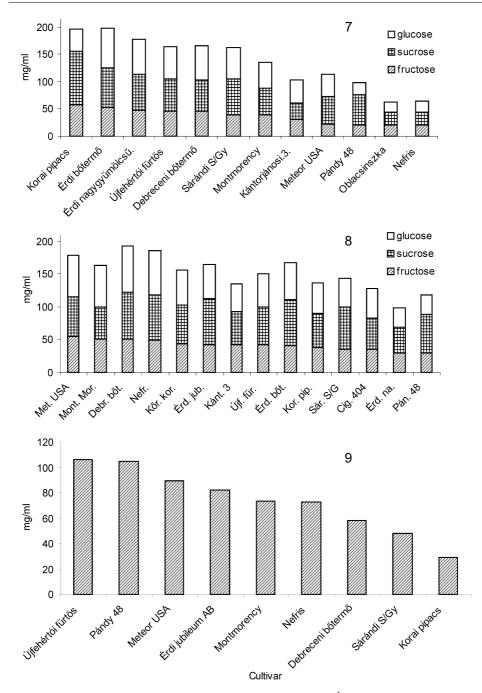
The ranking based on fructose content takes into consideration human sensation of taste. Part of honey made of sour cherry nectar is used for brood, but a certain amount of it may get into honey consumed by man, if bee families do not use the total amount of it. There is a remarkable variability in the fructose content of studied cultivars: in 1997 the nectar of 3 cultivars contained less than 20 mg/ml fructose, the others all exceeded it (Fig. 5). The nectar of 'Korai pipacs', which contained the least fructose among the cultivars in 1997, had the highest values in 1998 and 1999 (Figs 6–7). The nectar of the other cultivars did not reach or slightly exceeded 10 mg/ml fructose in 1998. The amount of fructose approached or exceeded 50 mg/ml in most cultivars in 1999 and 2000, thus sour cherry nectars were the sweetest in these two years from the viewpoint of human taste (Figs 7–8). In 1999 the following cultivars had less sweet nectar: 'Kántorjánosi 3', 'Meteor USA', 'Pándy 48', 'Oblacsinszka' and 'Nefris' (Fig. 7), in 2000: 'Sárándi S/Gy', 'Cigány 404', 'Érdi nagygyümölcsű' and 'Pándy 48' (Fig. 8).

Based on total sugar content the cultivars could be ranked as follows: in 1997 from 9 sour cherry cultivars 'Újfehértói fürtös' and 'Pándy 48' had the

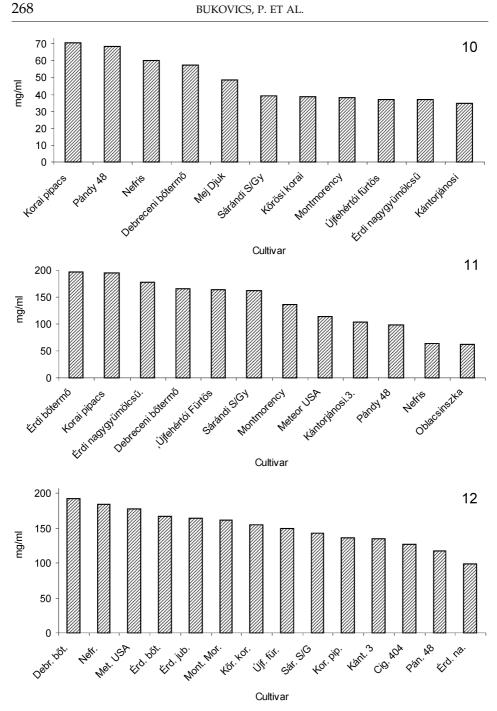
most concentrated nectar, these two cultivars reaching the concentration around the apicultural threshold value (100 mg/ml, corresponding to 10% refraction). The most dilute nectars were found in 'Korai pipacs', 'Sárándi S/Gy' and 'Debreceni bőtermő'. The nectar of 'Érdi jubileum AB', 'Meteor USA', 'Montmorency' and 'Nefris' was also dilute, with a sugar concentration between the two extremities, not preferred by bees (Fig. 9). In 1998 the nectar in none of the cultivars reached the bee visitation threshold (Fig. 10). The years 1999 and 2000 proved to be the most favourable for the sugar content of sour cherry nectar (Figs 11–12). From the studied cultivars the concentration of 100



*Figs* 5–6. Nectar sugar composition of sour cherry cultivars on the basis of fructose content at Újfehértó: 5 = 1997, 6 = 1998



*Figs* 7–9. Nectar sugar composition of sour cherry cultivars (at Újfehértó): 7–8 = on the basis of fructose content, 7 = 1999, 8 = 2000, 9 = on the basis of total sugar content, 1997



Figs 10-12. Nectar sugar composition of sour cherry cultivars on the basis of total sugar content at Újfehértó: 10 = 1998, 11 = 1999, 12 = 2000

mg/ml was not reached by the nectar of only two cultivars, 'Nefris' and 'Oblacsinszka' in 1999, and only one cultivar, 'Érdi nagygyümölcsű' in 2000; the floral secretory product of all other cultivars reached the threshold of bee visitation.

Following the classification by Baker and Baker (1990) the majority of the studied sour cherry cultivars belonged to the sucrose-rich category in 1997, based on their nectar composition. The floral secretory product of a single cultivar 'Érdi jubileum' was sucrose-dominant: S/(G+F) = 1. Among those with a sucrose-rich nectar the lowest values were found in 'Nefris' and 'Pándy 48'. The nectar of the other cultivars in ascending order of the quotient: 'Újfehértói fürtös', 'Sárándi S/Gy', 'Meteor USA', 'Montmorency',: 'Korai pipacs', 'Debreceni bőtermő'. The two values approaching 1 most closely belonged to nectars with the lowest concentration: 'Debreceni bőtermő' and 'Korai pipacs' (Table 1).

Based on the S/(G+F) the nectar of one cultivar ('Érdi nagygyümölcsű') was sucrose-dominant in 1998, while one cultivar ('Korai pipacs') could be classified into the hexose-rich group. The quotient of the other cultivars in ascending order: 'Pándy 48', 'Nefris', 'Debreceni bőtermő', 'Montmorency', 'Újfehértói fürtös', 'Sárándi S/Gy', 'Kőrösi korai', 'Mej Djuk' and 'Kántorjánosi 3' (Table 1). Interestingly, the ranking is almost the opposite considering the total

1997–2000					
Cultivar	1997	1998	1999	2000	
Cigány 404	-	-	-	0.58	
Debreceni bőtermő	0.95	0.74	0.53	0.60	
Érdi bőtermő	-	-	0.58	0.72	
Érdi jubileum AB	1.00	-	-	0.73	
Érdi nagygyümölcsű	-	1.03	0.59	0.65	
Kántorjánosi 3	-	0.98	0.42	0.59	
Korai pipacs	0.93	0.43	0.98	0.59	
Kőrösi korai	-	0.95	-	0.61	
Mej Djuk	-	0.96	-	-	
Meteor USA	0.79	-	0.83	0.51	
Montmorency	0.83	0.76	0.56	0.42	
Nefris	0.59	0.63	0.63	0.60	
Oblacsinszka	-	-	0.63	-	
Pándy 48	0.65	0.61	1.27	1.01	
Sárándi S/Gy	0.76	0.85	0.67	0.82	
Újfehértói fürtös	0.75	0.84	0.57	0.62	

Table 1

Nectar sugar composition of sour cherry cultivars on the basis of S/(G+F). Újfehértó, 1997–2000

sugar concentration and the quotient S/(G+F), *i.e.* the most concentrated nectars had the smallest quotient, whereas the most dilute nectars can be matched with the sucrose-dominant group (Fig. 10, Table 1).

Also in 1999 only one cultivar belonged to the sucrose-dominant category, but with an exceptionally high value: 'Pándy 48'. At the other end a hexose-rich cultivar can also be found: 'Kántorjánosi 3'. The floral secretory product of the other cultivars is sucrose-rich, the quotient being relatively high in the case of 'Korai pipacs' and 'Meteor USA', while the others are more or less similar. In ascending order: 'Debreceni bőtermő', 'Montmorency', 'Újfehértói fürtös', 'Érdi bőtermő', 'Érdi nagygyümölcsű', 'Oblacsinszka', 'Nefris' and 'Sárándi S/Gy' (Table 1).

In 2000 the nectar of one cultivar, 'Pándy 48' was sucrose-dominant, while the floral secretory product of 'Montmorency' belonged to the hexoserich group. From cultivars with a sucrose-rich nectar 'Sárándi S/Gy', 'Érdi jubileum' and 'Érdi bőtermő' had the highest values. The quotient of the floral secretory product in the other cultivars was around 0.6, thus could be classified into the sucrose-rich group (Table 1).

Climatic data (air temperatures and precipitation) explain the variation in nectar concentration more or less. In 1997, following a little precipitation, daily air temperatures were 22–26 °C, and nectars with a medium concentration were produced in this season. In 1998 little precipitation was accompanied by low air temperatures: 5.56–18.19 °C. In this season with cool weather the nectar of no cultivar reached the apicultural threshold value, concerning neither sucrose, nor total sugar. In 1999 abundant precipitation and changeable weather characterised the flowering period. Air temperatures varied between 0–21 °C, nectar concentration was high, on the basis of sucrose content the nectar of only 3 cultivars out of 12 did not reach the concentration preferred by bees. The secretory product was advantageous also considering total sugar content, which did not reach the threshold in two cultivars only. Year 2000 was the hottest, air temperatures being 12.7–25.9 °C, with nectar values similar to the previous year. In this season there was no precipitation before and during blooming.

Concerning all the above aspects, the following cultivars proved to be the most valuable ones from an apicultural point of view: 'Újfehértói fürtös', 'Pándy 48', 'Érdi jubileum' and 'Érdi bőtermő'. These cultivars yielded nectar with high sucrose content in each season, even under varying climatic conditions.

*Acknowledgement* – This research work was supported by the Hungarian Scientific Research Fund (OTKA grant No. T 023203).

#### REFERENCES

- Baker, H. G. and Baker, I. (1983a): A brief historical review of the chemistry of floral nectar. In: Bentley, B. and Elias, T. (eds): Biology of nectaries. Columbia University Press, New York, pp. 126–152.
- Baker, H. G. and Baker, I. (1983b): Floral nectar sugar constituents in relation to pollinator type. – In: Jones, C. E. and Little, R. J. (eds): Handbook of experimental pollination biology. Van Nostrand-Reinhold, New York, pp. 117–141.
- Baker, H. G. and Baker, I. (1990): The predictive value of nectar chemistry to the recognition of pollinator types. *Israel J. of Bot.* **39**: 157–166.
- Benedek, P. and Nyéki, J. (1997): Considerations on the nectar production and the honeybee visitation of fruit tree flowers. *Horticultural Science Kertészeti Tudomány* **29**(3–4): 117–122.
- Botz, L., Orosz-Kovács, Zs., Erdős, Z., Timon, B., Majerné Bordács, M. and Farkas, Á. (2003): Prunoideae gyümölcsfajták nektárösszetétele. (Nectar composition of fruit cultivars in Prunoideae.) – *Bot. Közlem.* (in press).
- Frisch, K. (1950): Bees: their vision, chemical senses and language. Cornell Univ. Press, Ithaca, N.Y.
- Gulyás, S. (1975): *A méhlegelő.* In: Halmágyi, L. and Keresztesi, B. (eds): A méhlegelő. Akadémiai Kiadó, Budapest, pp. 21–92.
- Kartasova, N. N. (1965): Sztroenije i funkcija nektarnikov cvetka dvudolnüh rasztenij. Izdatelsztvo Tomszkogo Universiteta, Tomszk.
- Maurizio, A. (1960): Biene und Bienenzucht. Kapitel Bienenbotanik, München.
- Majer-Bordács, M., Botz, L., Orosz-Kovács, Zs. and Kerek, M. M. (1993): *The composition of nectar in apricot cultivars.* – Acta Horticulture, Tenth Intern. Symp. Apricot Culture, Izmir, Turkey, pp. 367–371.
- Majer-Bordács, M., Orosz-Kovács, Zs., Gulyás, S. and Erdős, Z. (1989): Szilvafajták nektárprodukciója és annak taxonómiai jelentősége. A biodiverzitás tanulmányozásának módszerei és eredményei. – Poszterkivonatok, Budapest, p. 14.
- Orosz-Kovács, Zs. (1991): A cseresznye és a meggy nektáriumstruktúrája és nektárprodukciója. Kandidátusi disszertáció, Pécs, 87 pp.
- Orosz-Kovács, Zs., Szabó, L. Gy., Bubán, T., Farkas, Á. and Bukovics, P. (2000): Sugar composition of floral nectar in sour cherry cultivars. – *Intern. J. Horticultural Science* **6**(3): 109–114.
- Örösi, P. Z. (1968): Méhek között. Mezőgazdasági Kiadó, Budapest.
- Percival, M. S. (1961): Types of nectar in Angiosperms. New Phytol. 60: 235-281.
- Simidtschiev, T. (1972): Prinosz kom proucsvane nektaroproduktivnosztja i medoproduktivnosztja na szlivata (Prunus domestica). – *Naucsni Trudove, Zsivotnovodsztvo, Viszs. Szelkosztopanszki Insztitut V. Kolarov, Plovdiv* **21**(5): 97–107.
- Terpó, A. (1980): *Virágbiológiai alapismeretek.* In: Nyéki, J.: Gyümölcsfajták virágzásbiológiája és termékenyülése.) Mezőgazdasági Kiadó, Budapest.
- Wykes, G. R. (1952): The influence of variations in the supply of carbohydrate on the process of nectar secretion. *New Phytol.* **51**(3): 294.