THE STRUCTURE OF FLORAL NECTARIES OF SOME SPECIES OF *VICIA* L. (PAPILIONACEAE)

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(Received: March 7, 1995. Accepted: October 3, 1995)

ABSTRACT

The subject of research were morphology and ultrastructure of floral nectaries of nine species of *Vicia*. The differences in their size and morphological structure were shown. Small, almost flat nectaries appeared in flowers of *Vicia tetrasperma* and *V. hirsuta*. Much better developed ones which had convexities with the shape of a protuberance, a half-ring or a half-ring with a ligulate outgrowth were observed in *V. silvatica*, *V. cracca*, *V. villosa*, *V. sativa* and *V. angustifolia*. Completely convex, annular nectaries with a ligulate outgrowth belonged to *V. sepium* and *V. grandiflora*. Small anatomical differences concerned mainly the structure and distribution of vascular bundles, whereas ultrastructure of secretory cells was very similar. Nectar got into the surface through the modified stomata situated on the top of nectaries' convexities.

KEY WORDS: *Vicia*, nectaries, anatomy, morphology, ultrastructure.

INTRODUCTION

Problems connected with the process of nectaring were subject of a lot of research undertaken in recent years. The obtained results show essential differences in the quantity and quality of a secreted nectar. They are very often caused by a different structure of nectaries within a genus (Gulyas and Kincsek 1982, Gulyas et al. 1976) or even among varieties and cultivars of the same species (Teuber et al. 1980, Samataro et al. 1985, Davis and Gunning 1991).

The nature of secretory processes in nectaries is not up to now sufficiently known. On the basis of anatomical structure and ultrastructure, sometimes with the aid of cytochemical methods, the ways of pre-nectar transport to the surface of a nectary were examined (Meyberg and Kirsten 1981, Gunning and Hughes 1976, Pate et al. 1985, Robards and Oates 1986, Davis et al. 1988, Sawidis 1991, Sawidis et al. 1987, 1989, Zer and Fahn 1992). The attempts have also been made to define the model of nectar secretion from secretory cells – granulocrine or eckerine secretion (Rachmilevitz and Fahn 1973, 1975, Fahn 1979, Kronstedt and Robards 1987, Robards and Stark 1988).

Thus far the trichome nectaries of *Abutilon* and *Hibiscus* are the best examined. There appeared some papers concerning *Vicia faba* nectaries also. However, the data about the secretory structures of other species of the genus *Vicia* are incomplete and the purpose of this study was the examination and comparison of morphology, anatomy and ultrastructure of floral nectaries of nine species of vetch commonly found in Poland. The results and an analysis of nectaring will be used to estimate the apiarian value of these plants.

MATERIAL AND METHODS

The studies were carried on floral nectaries of the following species of the genus *Vicia* L. (Papilionaceae): *Vicia hirsuta*, *V. tetrasperma*, *V. silvatica*, *V. cracca*, *V. villosa*, *V. sepium*, *V. sativa*, *V. angustifolia*, *V. grandiflora*.

The glands removed from flowers during the phase of secretory activity were fixed in a buffered 3% glutaraldehyde for 4 hours in the room temperature. After several washings in 0.1 M phosphate buffer (pH 7.0) the material was subjected to postfixation in 2% osmium tetroxide for 4 hours at 4°C.

Nectaries for a scanning electron microscope (SEM) were dehydrated in ethanol series and then in acetone, and they were dried in a critical point of CO₂. After coating with gold the surface of nectaries was observed through the microscope type BS-340 TESLA at the voltage 25 KV.

The fixed and dehydrated material was also embedded in epoxy resin (Spurr 1969) and cut with a glass knife into ultrathin sections which were stained according to Reynold's (1963) method. Then they were examined with a transmission electron microscope (TEM), type BS-500 TESLA at the voltage 90 KV.

The specimens for a light microscope (LM) were prepared by means of a paraffin method but instead paraffin HISTO-SEC was used. The 10-15 µm thick sections, cut with a steel knife were stained with a 0.05% toluidine blue O. The fresh nectaries cut by hand were tested for the presence of starch, cutinized and lignified cell-walls by means of JKJ, Sudan III and floroglucine with HCl, respectively.

The number of secretory stomata was determined as an average from 5 nectaries observed in SEM. The thickness and number of cells layers of a secretory parenchyma is the result

of measuring of 10 nectaries cut into semi-thin sections and observed in LM.

RESULTS

Floral nectaries of the examined species of vetch were put at the receptacle around the base of ovary or androecium. They were surrounded by a tube of nine fused staminal filaments and on the standard side at the base of the tenth, free stamen there were two openings leading to a nectarous chamber. Nectaries of individual species were different both in shape and in size (tab. 1). The smallest glands appeared in very small flowers of *V. tetrasperma* and *V. hirsuta*. In *V. tetrasperma* they were almost flat with a small convexity on the side of staminal tube. At its top there were modified stomata, called secretory stomata (Fig. 1). The nectary of *V. hirsuta* was the only, among the examined species, which was situated at the base of a staminal tube, where it was visible as a

small, half-ring protuberance covered with secretory stomata (Fig. 2).

Much bigger glands appeared in flowers of the remaining species. The flat nectary of *V. silvatica* had a protrusion on the receptacle on the side of staminal tube (Fig. 3), and in *V. cracca* and *V. villosa* in the analogous place there was a half-ring comprising the base of ovary (Fig. 4, 5, 6). Most of secretory stomata at the top of nectaries' convexities were open, but very few closed ones were observed too. In *V. angustifolia* and *V. sativa* the half-ring of a nectary had a ligulate outgrowth with secretory stomata on the top. It was more prolonged and narrow in *V. sativa*, whereas a shorter and wider one in *V. angustifolia* (Fig. 7, 8). The biggest nectaries appeared in flowers of *V. sepium* and *V. grandiflora*. They had a shape of a big ring surrounding the base of ovary. They also had ligulate outgrowths on the side of a staminal tube (Fig. 9).

The cells of nectary's epidermis, mainly isodiametrical and slightly convex, had a smooth surface. Only near secretory stomata they were prolonged and were covered with a thick,

(Figs 1-4). Longitudinal sections of nectaries, LM.

Fig. 1. Flat nectary of *V. tetrasperma* visible on both sides of an ovary. Secretory stoma is marked with an arrow, 235x.

Fig. 2. Nectary of *V. hirsuta* situated at the base of a staminal tube. Secretory stoma is marked with an arrow, 200x.

Fig. 3. Convex fragment of the nectary of *V. silvatica* with a secretory stomata on the top (arrow), 210x.

Fig. 4. Receptacle of *V. cracca* with a flat part of nectary visible at the base of a free stamen and a convex one, on the side of staminal tube, 100x.

Abbreviations:

N – nectary, G – ovary.

(Figs 5-10). Morphology of nectaries, SEM.

Fig. 5. Nectary of *V. villosa* with a flat fragment on the side of a free stamen and with a half-ring surrounding the base of ovary, 230x.

Fig. 6. Fragment of a half-ring of *V. cracca* nectary with secretory stomata on the top (arrow), 530x.

Fig. 7. Arrangement of nectary on the receptacle of *V. sativa*. A long, ligulate outgrowth is situated on the side of staminal tube, 98x.

Fig. 8. Ligulate outgrowth of *V. angustifolia* nectary with secretory stomata on the top, 320x.

Fig. 9. Nectary of *V. grandiflora* with the shape of a big ring surrounding the base of ovary with ligulate prolongation on the side of staminal tube, 78x.

Fig. 10. Secretory stomata on the top of *V. sepium* nectary's ligule. The cells of epidermis around them are prolonged and covered with cuticle of undulating surface.

Abbreviations:

N – nectary, G – ovary, A – filament of a free stamen,

TABLE 1. Comparison of some anatomical features of floral nectaries of *Vicia* sp.

Species	Nectary's disk			Disk's outgrowth		
	Number of cells layers	Thickness of nectary's tissue [μm]	Vascular bundle ¹⁾	Height [μm]	Number of secretory stomata	Vascular bundle
<i>V. hirsuta</i>	4	60	F	40	6	–
<i>V. trasperma</i>	4	82	FK	85	9	–
<i>V. silvatica</i>	6	85	FK	135	12	–
<i>V. cracca</i>	6	90	F	200	18	F
<i>V. villosa</i>	6	90	F	200	20	F
<i>V. sepium</i>	15	180	F	350	28	F
<i>V. sativa</i>	10	120	F	280	25	F
<i>V. angustifolia</i>	10	120	F	230	23	F
<i>V. grandiflora</i>	12	160	F	300	31	F

¹⁾ F – phloem, K – xylem

undulating cuticle (Fig. 10). The surface of the cells of epidermis did not contain pores or cracks, and the only visible way for nectar escape were secretory stomata.

On histological specimens the dense nectary's tissue was clearly distinct from its adjacent parenchyma. There were differences among individual species in its thickness and the

number of secretory parenchyma cells layers (table 1). These cells were small, isodiametrical with relatively thick, cellulose walls. They usually had a few small vacuoles, a big nucleus and cytoplasm which intensively stained with toluidine blue. Numerous starch grains were found in guard cells and in the neighbourhood of vascular bundles inside a nectary, where

(Figs 11-13). Vasculature of nectaries of *Vicia*, LM (longitudinal sections).

Fig. 11. Flat fragment of nectary's disk of *V. villosa* with phloem endings right under secretory tissue (arrow), 300x.

Fig. 12. Nectary's ligule of *V. sepium* with elements of phloem inside (arrow), 200x.

Fig. 13. Nectary's ligule of *V. angustifolia* with phloem inside (arrow), 180x.

Abbreviations:

N – nectary

there were often single crystals of calcium oxalate also. Nectaries' vascular bundles branched from staminal sheath ones. In nectaries of *V. hirsuta* and *V. silvatica* they consisted of phloem as well as of xylem and in other species – phloem only. In flat fragments of glands they ended immediately under the secretory tissue, whereas all convexities had the vascular tissue inside (Fig. 11, 12, 13).

The nectaries of the examined species of vetch had a lot of common features of submicroscope structure. The cells of epidermis had a parietally situated cytoplasm with single chloroplasts, a small number of mitochondria and ER tubules. Big vacuoles were most commonly electron-empty or contained flocky precipitates. Under the epidermis there were intercellular spaces, especially big beneath secretory stomata, but in deeper layers of the nectaries' cells they were not visible (Fig. 14). The cell-walls, both of epidermis and of secretory parenchyma were smooth or slightly undulating. Only in *V. grandiflora* small wall ingrowths were observed (Fig. 15). The cells of secretory parenchyma were weakly vacuolised. In cytoplasm there were numerous ribosomes and short ER tubules. Small vacuoles of *V. villosa* cells contained globules of dark coloured substance (Fig. 16). A lot of vesicles with bright content, sometimes surrounded by a common membrane creating multivesicular bodies, gathered together with mitochondria along plasmalemma (Fig. 17). The plasma membrane most commonly had undulating shape and many convexities (Fig. 18). The Golgi apparatus in secretory cells was observed sporadically. Plasmodesmata appeared in great number in walls of deeper situated cells of secretory parenchyma – both tangent and radial to the surface of a nectary. Much more seldom they were observed among the cells of epidermis and in the first layer of parenchyma underneath.

DISCUSSION

Floral nectaries of *Vicia* L. had a typical structure for the *Papilionaceae* family. They belong to a discoidal type which in this genus was described by Moore (1936), Fahn (1953), Rao (1971), Waddle and Lersten (1973).

The results obtained in the present work, concerning morphological and anatomical structure of nectaries, do not confirm the observations of Gulyas et al. (1976) and Gulyas and Kincsek (1982). These authors examined floral nectaries of 45 members of *Papilionaceae*, among others some species of vetch. They observed that in *V. villosa*, *V. sepium* and *V. angustifolia* appeared epimorphic, flat nectaries, with no vascular bundles. Species with this kind of glands were classified as the least nectaring. Automorphic, convex nectary, with a shape of a symmetrical ring around an ovary, inside which there were bundles of phloem, was described for *V. cracca* by these authors. The nectary in flowers of *V. sativa* was presented as a ring with a ligulate outgrowth which had bundles built of phloem and xylem. This species was classified as the best nectaring one.

The connection between nectar secretion and the structure of a vascular bundle of a nectary was noted by Frei (1955) and Frey-Wyssling (1955). They observed that nectaries supplied by phloem produced a nectar with a high concentration of sugars. The glands with bundles built of phloem and xylem, especially when xylem dominated, produced a lot of nectar with a low content of sugars.

In *Vicia* nectaries secretion into the surface took place through the modified stomata which were situated on the top of a nectary's convexity, in the way similar to broad bean (Davis

et al. 1988, Davis and Gunning 1991, 1992). The number of secretory stomata in various species of vetch was different, but it was certainly connected with the size of a nectary, similarly to lines or cultivars of *Helianthus* (Samataro et al. 1985). Davis and Gunning (1991) noted also that *V. faba* cultivars with the longest disk's ligulas had a greatest number of secretory stomata. However, in the case of *Lotus corniculatus* (Murrel et al. 1982) and *Vicia faba* (Davis and Gunning 1991) the connection between the number of secretory stomata and the volume of secreted nectar or a potential amount of sugars in nectar finally was not confirmed.

The majority of the observed secretory stomata of vetch were open, as in nectaries of other plants. Teuber et al. (1980) noted that in alfalfa they remain always open, because they have no ability to move, even after being subjected to various stimuli, which normally cause movement of guard cells of leaves. However, in secretory active glands of *V. cracca* and *V. villosa* appeared also closed stomata similarly to bean (Webster et al. 1982) and broad bean (Davis and Gunning 1992), where they were observed in all stages of nectary's development. Because they have no ability to actively regulate a pore and their development is not closely correlated with a secretory stage, Davis and Gunning (1992) suggest that the nectar flow is not at all regulated by secretory stomata.

The structure of vetch's nectaries cells showed characteristic features for this type of secretory tissues (Fahn 1979, Durkee 1983) and in individual species they were essentially similar. Their walls had mainly smooth and slightly undulating shape. Little ingrowths were observed only in *V. grandiflora*. However, Davis et al. (1988) noted in *Vicia faba* wall ingrowths both in epidermis and in subepidermal cells, especially around intercellular spaces. Similar wall protuberances appeared in the floral nectaries of *Brassica* (Davis et al. 1986), and sepal nectaries of *Banana* (Fahn and Benouaiche 1979), *Gasteria* and *Aloë* (Schnepf and Pross 1976). Wall ingrowths are characteristic structures of transfer cells which mainly due to the fact that they increase the surface of plasmalemma, improve an intensive transport on short distances (Gunning and Pate 1969, Pate and Gunning 1972). They, however, do not appear in the walls of all floral nectaries. They were not found in *Vinca* and *Citrus* (Rachmilevitz and Fahn 1973), *Passiflora* (Durkee 1981), *Aptenia* (Meyberg and Kirsten 1981), *Trifolium* (Eriksson 1977).

On the surface of plasmalemma of nectary cells of vetch numerous convexities appeared, whereas along it a lot of small vesicles gathered. They presumably came from a well-developed system of ER membranes. The participation of ER tubules and vesicles in secretory processes was confirmed by experiments with labelled sucrose (Fahn and Rachmilevitz 1975) and by the fact that in these structures high activity of acid phosphatases was observed (Fahn and Rachmilevitz 1975, Heinrich 1975). The involvement of ER in nectar secretion is emphasized also by Davis et al. (1988), Robarts and Stark (1988), Sawidis et al. (1989), Arumugasamy et al. (1990), Sawidis (1991). There are also known the examples of nectaries which cells have a very weakly developed system of ER membranes – *Aptenia cordifolia*, (Meyberg and Kirsten 1981), or it was noticed that no secretory active vesicles formed out of ER – *Trifolium* (Eriksson 1977), *Passiflora* (Durkee 1981), *Strelitzia* (Kronstedt and Robards 1987). Few authors think that the Golgi apparatus also takes part in the process of accumulation and nectar secretion (Schnepf 1977, Fahn 1979). Other works showed that the main role of the Golgi vesicles is providing polysaccharides for the synthesis of walls' ingrowths which form themselves before the beginning of secretion (Schnepf and Pross 1976).

(Figs 14-18). Ultrastructure of nectaries of *Vicia*, TEM.

Fig. 14. Fragment of *V. tetrasperma* nectary with the epidermis and underlying secretory parenchyma cells much more vacuolised than those of deeper strates. Intercellular spaces (asterisks) are situated beneath epidermis, 7000x.

Fig. 15. Secretory parenchyma cell of *V. grandiflora* with ingrowths of walls (arrow), 10000x.

Fig. 16. Small vacuoles with a dark globules and many bright vesicles in cytoplasm of secretory parenchyma cell of *V. villosa*, 20000x.

Fig. 17. Cytoplasm of a cell of secretory parenchyma of *V. villosa* with numerous vesicles and short ER tubules. Some vesicles are surrounded by a common membrane. Plasmodesmata in a wall are marked with an arrow, 20000x.

Fig. 18. Cytoplasm of *V. angustifolia* secretory parenchyma cell with numerous vesicles and short tubules of ER. Plasmalemma possesses a characteristic undulating profile (arrow), 15000x.

Abbreviations:

V – vacuole, m – mitochondrion, W – cell-wall, ER – endoplasmic reticulum, n – nucleus, E – epidermis

On the basis of ultrastructure of nectaries of vetch we may think that, similarly to broad bean (Davis et al. 1988), there are two possible ways of nectar's transport: 1) symplastic – through plasmodesmata and 2) apoplastic – in walls and intercellular spaces. Because there are numerous vesicles in the cytoplasm of secretory parenchyma's cells, especially near plasmalemma, they probably take part in secretory processes. However, in order to confirm this the precise cytochemical analyses should be carried out.

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BUDOWA NEKTARNITÓW KWIATOWYCH KILKU GATUNKÓW
Z RODZAJU *VICIA* L. (*PAPILIONACEAE*)

STRESZCZENIE

Przedmiotem badań była morfologia, anatomia i ultrastruktura nektarników kwiatowych dziewięciu gatunków wyki. Wykazano różnice w ich wielkości i budowie morfologicznej. Niewielkie, prawie płaskie nektarniki występowały w kwiatach *Vicia tetrasperma* i *V. hirsuta*. Znacznie lepiej wykształcone, z wypukłościami w postaci wzgórka, półpierścienia lub półpierścienia z języczkowatym wyrostkiem obserwowano u *V. silvatica*, *V. cracca*, *V. villosa*, *V. sativa* i *V. angustifolia*. Całkowicie wypukłe, pierścieniowate nektarniki z języczkowatym wyrostkiem należały do *V. sepium* i *V. grandiflora*. Niewielkie różnice anatomiczne dotyczyły głównie budowy i rozmieszczenia wiązek przewodzących, natomiast ultrastruktura komórek wydzielniczych była bardzo zbliżona. Nektar wydostawał się na powierzchnię przez zmodyfikowane aparaty szparkowe znajdujące się na szczycie wypukłości nektarników.

SŁOWA KLUCZOWE: *Vicia*, nektarniki, anatomia, morfologia, ultrastruktura.