ANATOMICAL STRUCTURE AND SURFACE MICROMORPHOLOGY OF TOMATILLO LEAF AND FLOWER (*PHYSALIS IXOCARPA* BROT., SOLANACEAE)

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ABSTRACT

Tomatillo (*Physalis ixocarpa* Brot.) is a newly introduced cultivated plant in Poland. Its anatomy was investigated in light and scanning electron microscopes. Tomatillo adult leaf had one layer of palisade parenchyma. The 1-2 cell layers of spongy parenchyma situated just below the palisade parenchyma showed large, tightly packed cells with great druses. The remaining spongy parenchyma was built of cells showing several extensions. Peculiarity of the sepals were the stomata situated on columns or hills formed of many cells. The petals had a very loose mesophyll. Their adaxial epidermis was composed of papillate cells. Such structure of the petal epidermis probably contributes to light dispersion and prevents glittering. There were several types of trichomes on the leaves, sepals and petals, some of them glandular and some simple. The large, very ramified, dendritic trichomes situated on the petals at the entry to the ovary might eventually protect it against excessive drying. The pollen grain was spherical, three-colpate. The style had a hollow channel inside. The stigma was of a wet, papillate type. Sometimes thorny trichomes were found among papillae.

KEY WORDS: leaf anatomy, flower anatomy, surface micromorphology, trichomes, pollen grain, *Physalis ixocarpa*.

INTRODUCTION

Tomatillo is an important vegetable crop in Mexico. Its cultivation spreads also gradually to other countries (Jankiewicz and Borkowski 1990, Moriconi et al. 1988, Abak et al. 1994). This species shows great ability to adapt to different climatic conditions and may be cultivated in the subtropics from which it originates as well as in the vicinity of Moscow and Sankt Petersburg (Medvedev 1958). In temperate climate it is cultivated mainly from transplants, similarly like tomato (Jankiewicz et al. 1989). It has been recently shown that tomatillo fruit does not contain harmful substances (Drost-Karbowska et al. 1993) and its nutritive value is comparable to that of tomato fruit (Ostrzycka et al. 1988). The plant is relatively resistant to pests except viruses. Nevertheless several tomatillo forms exhibiting good tolerance to virus diseases have been found (Fiedorow and Jankiewicz 1993).

Only few investigations are known from literature on the biology of tomatillo (Mulato Brito et al. 1985, Cartujano Escobar et al. 1987, Jankiewicz et al. 1989). The anatomy and micromorphology of tomatillo fruit was investigated by Dyki et al. (1997). We have not found any paper concerning the anatomy and surface micromorphology of tomatillo leaf and flower therefore our paper deals with this topic.

General structure of the leaf is discussed in a number of textbooks e.g. by Esau (1965) and Malinowski (1980). These authors present also the data concerning leaf anatomy of plants belonging to Solanaceae, like tobacco and potato. Leaf structure is variable and depends greatly on illumination and water stress (Igboanugo 1992, Bussotti et al. 1995), as well as

on the level of growth regulators (Bosabalidis and Exarchou 1995).

The microstructure of petals and sepals has been rarely investigated. The basic data were given by Esau (1965). The classification of different types of styles and their stigmas has been presented by Heslop-Harrison and Shivanna (1977).

The surface micromorphology of above-ground parts of plants attracts recently the attention of investigators. The structure and biochemistry of plant surface are important for the pesticide industry since the formulation of a pesticide must be adapted to the surface properties of a given plant (McWhorter et al. 1993). The presence of trichomes and their structure is important from the point of view of taxonomy (Hardin 1979, Metcalfe and Chalk 1979, Poston and Nowicke 1993). Glandular trichomes seem to play an important role as the first defense against insects and diseases (Gibson 1971, Wagner 1991). In *Lycopersicon esculentum* x *L. hirsutum* hybrids the resistance to mites was closely correlated with the density of a certain type of trichomes (Good and Snyder 1988). In the glandular trichomes, the exudate is usually accumulated between the cuticle and the cell wall (Fahn 1988, Ferreira and Janick 1995).

Although the anatomy and surface micromorphology of tomatillo flower has not yet been investigated, there are some data on the flowers of closely related Solanaceae species (Johri et al. 1992). The study of the structure of the stigma surface may contribute to understanding the problems of pollination and self-incompatibility (Heslop-Harrison 1975). The structure of the pollen grain may be important for plant hybridization and taxonomy (Knox 1984).

MATERIAL AND METHODS

The plants from which the material was collected for this investigation were cultivated in the experiment field in Wolica of the Warsaw Agricultural University. The material originated from 5 plants. Stamens, anthers and fragments of central part of leaves (0.5-1 cm²), calyx and corolla were fixed in CrAF and dehydrated in series of ethanol:water solutions ending with absolute ethanol (Gerlach 1972). This material was divided into two parts. One part was embedded in paraffin for anatomical investigations in light microscope Nu-1, Zeiss (LM). The paraffin sections were stained in 2% safranin and 1% light green in ethanol. Another part of the fixed in CrAF material was dried in liquid CO₂ at critical point, sputter coated with gold-palladium and observed with the aid of Jeol JSM-1 scanning electron microscope (SEM) (Hayat 1976). The details of the methods were given when necessary with the results.

RESULTS

Anatomy of the leaf

The mesophyll of the relatively young leaf (40-45% of final size) was built of closely packed cells. This is a typical structure in this stage of development (Maksymowycz and Erickson 1973). There was only one layer of palisade parenchyma and about 5 layers of spongy parenchyma. In an older but not yet mature leaf (Fig. 1) the epidermal cells on the adaxial side were larger than those on the abaxial side. There has been still only one layer of palisade parenchyma but the spongy parenchyma was somewhat looser than before. The spongy parenchyma cells situated just below the palisade parenchyma were larger than the cells in other spongy parenchyma layers (Fig. 1). The larger veins (Fig. 2) were bicollateral, surrounded with bundle sheath contacting both adaxial and abaxial epidermis. The small veins were situated just beneath the palisade parenchyma or beneath the upper layer of spongy parenchyma.

The palisade parenchyma of the mature leaf (Figs 3, 3a and 3b) was composed of one layer of very elongated, sometimes ramified cells. In the spongy parenchyma the first 1-2 layers of cells situated just below the palisade parenchyma (we will refer to them as "upper spongy parenchyma") were different from the others. The cells of these 1-2 layers were very large, mostly oval-like and sometimes irregular in shape. Most of them contained large druses shining in polarized light. Smaller druses were often found in palisade parenchyma and less often in the lower spongy parenchyma. The cells in the lower spongy parenchyma were showing several side extensions and were rather densely arranged.

Surface micromorphology of the leaf

The surfaces of both sides of the leaf did not differ markedly. Stomata were present on both of them (Figs 4, 5 and 6). The outlines of the epidermal cells visible on the leaf surface were polygonal and usually isodiametrical except the cells accompanying the larger veins which were elongated in a parallel manner to the course of the vascular bundle (Fig. 4). The cells were convex but the stomata were situated in shallow depressions. The trichomes were of three main types:

1. Ordinary, 1-4 celled, conical in shape, rarely ramified (Figs 4, 5a and 6). Sometimes their apical, smallest cell was filled with a dark substance which would indicate that they eventually were gradually transformed into a glandular form.

2. Glandular "club-like" hairs with a head composed of four cells with a "neck" built of few cells and one-cell stick (Figs 4, and 5).
3. At the margin of the leaf there were only short, simple, teeth-like, unicellular trichomes, conical, pointing toward the apex (Fig. 27). The trichomes on both sides of the leaf were more abundant along the veins (Fig. 4).

The flower

Tomatillo flower was perigynous with the superior ovary (Fig. 7, see also Dyki et al. 1997). The synsepalous calyx was formed of five, green sepals and the sympetalous corolla of five bright yellow petals with a dark blue or brownish patch near the base. In the androecium there were five stamens of different height. Their bases were fused with petals. They never reached higher than the stigma. The syncarpic ovary was usually composed of three carpels. The style was relatively long and rather thick (see Dyki et al. 1997).

The cross-sections of the sepal in an open flower and sepal surface view revealed that the epidermis on its both sides had rather isodiametrical cells (Figs 8-12). The arrangement of the cells (Fig. 11) in pairs and fourth suggest that many cells had freshly divided. The peculiarity of tomatillo is that the calyx continues intensive growth as well during flower development as after the fecundation forming the "fruit envelope" (Fig. 7, see also Dyki et al. 1997). The mesophyll of the sepal is not differentiated into palisade and spongy parenchyma (Fig. 8 and 8a).

The surface micromorphology of the abaxial side of the sepal of the open flower was presented in Figs 9-11. The epidermal cells were convex and rather isodiametrical. The trichomes were of three types, and two of them were similar to those of the leaf: the glandular "club-like" trichomes, and short, 1-3 celled, simple conical ones (Fig. 9). The third type were the long glandular 2-4 cellular hairs (Fig. 10). The hairs at the margin of the sepal were relatively small and ordinary (Fig. 27).

The peculiarity of the sepal surface were the stomata on the hills or columns built of many cells (Figs 8-11). The adaxial surface of the calyx envelope surrounding a half-grown fruit (Fig. 12) presented thick deposit of a wax-like substance covering the epidermis and causing that the contours of the cells were smudged.

The structure of tomatillo petal is very delicate (Figs 13 and 14). The epidermis is thin-walled. In the middle and upper part of the petal, almost each cell of the adaxial epidermis showed a papilla situated on the top of very convex outer tangential wall. The epidermal cells superposed over the larger veins had no papillae (Fig. 15). Some papillae were also encountered in the abaxial epidermis (Fig. 13 and 14). The mesophyll was very loose and the large intercellular spaces often have extended from the adaxial to the abaxial epidermis. The small vascular bundles did not show distinct bundle sheath, however the larger bundles did show it. The larger veins were bicollateral. There were several types of trichomes on the petals:

1. simple, 1-4 cellular, uniseriate, conical (Fig. 15), similar to those of a leaf and sepal (compare Figs 4, 5a, 6 and 9),
2. "club-like", glandular (Fig. 15), similar to those on the leaf and on the sepal (Figs 5 and 9-11).
3. uniseriate, glandular with a 1-2 cell head and a stick of about 1-5 cells, thickening toward the base (Fig. 15). The head was frequently filled with a dark substance (preparations without staining). At the margins of petals (Fig. 27) occurred densely the trichomes of the type "1" and "3",

Figs 1 and 2. The cross sections through the central part of a young tomatillo leaf (about 60-65% of final size). In Fig. 2 the cross-section of the lateral vein of the 1st order; ad – the adaxial side of the leaf, p – palisade parenchyma, us – upper spongy parenchyma, ls – lower spongy parenchyma, b – bundle sheath, e – bundle sheath extensions, x – xylem, f – phloem, v – vein of the high order (x 600).

Fig. 3. The cross section through the central part of a mature leaf. Note very long palisade parenchyma cells and large druses (d) in the upper spongy parenchyma cells. Explanations as for Fig. 1 and 2, (x 700).

Fig. 3a. The mature leaf cross section in polarized light to show the crystals and druses (d) which are shining in this light (x 600).

Fig. 3b. Upper spongy parenchyma cells of the mature leaf to show the rhombohedral crystals (o), (x 900).

Fig. 4. The abaxial surface of the leaf. Epidermal cells superimposed over the vein are elongated parallel to it. The trichomes: "club-like" and ordinary, unicellular, conical (compare Figs 5 and 6) were more frequent along the vein, (SEM, x 300).

Fig. 5. Adaxial surface of the leaf with a glandular "club like" trichome, note also the presence of stomate, (SEM, x 2000).

Fig. 5a. Types of trichomes occurring on the adaxial epidermis of a leaf along the main vein. The types marked with x are most common, v – club-like trichome (x 350).

Fig. 6. Adaxial surface of the leaf with a simple, unicellular, conical trichome and a stomate (SEM, x 1000).

Fig. 7. The developing, half-open, open (but starting to wilt) and wilted flowers of tomatillo x 1 (for a cross-section of the flower see also Dyki et al. 1997). Between the first and the last stages shown passed 7 days. Compare also Fig. 26 with fully open flower.

Fig. 8. and 8a. The cross-sections of the middle part of the sepal in an open flower, note the stomata on "hills" (sh), ad – adaxial side, ab – abaxial side, v – veins.

Fig. 9. The abaxial surface of the sepal of an open flower. Characteristic hills (columns) with the stomata (white stroke) and two types of trichomes: "club-like" (black stroke) and unicellular conical (triangles), (SEM, x 750).

Fig. 10. Other, large type of glandular trichomes (a stroke) on the abaxial surface of the sepal, (SEM, x 350).

Fig. 11. The same as in 9 magnified, stomata on the columns, (SEM, x 1200).

Fig. 12. The adaxial side of the calyx envelope of the half-grown fruit. The contours of the cells are smudged due to a heavy deposit of wax-like substance, (SEM, x 750).

Figs 13 and 14. The cross-sections through the central part of the petal. Note the epidermal cells with papillae on both sides of the petal. ad – adaxial side, v – the veins of the high order (in Fig. 13) and of the main order (in Fig. 14), b – bundle sheath, (x 600)

Fig. 15. Adaxial surface of the central part of the petal. The papillae (compare Fig. 13) occur on each cell except those superimposed over the vein; three types of trichomes are visible: "club-like" (an arrow), 1-2 cellular, ordinary, conical (a stroke) and glandular, uniseriate with one-cell-head and swollen basal cells (arrow head), (SEM, x 200).

Fig. 16. The cross-section through the anther, shortly before its opening; a stroke indicates dehiscence fissure, s – septum, en – endothecium, ep – epidermis, (x 300).

Fig. 17. Tissues of the anther near the dehiscence fissure (an arrow), note very large cells of epidermis (c) next to the cells closing the dehiscence fissure, (x 750).

Fig. 18. The pollen grain, (SEM, x 3000).

Fig. 19. The cross section through the style, (x 200). v – the vein, t – the tissue with small cells full of cytoplasm lining the channel (c).

Fig. 20. The longitudinal section through the stigma. Visible the stigma cavity (d) and the fragment of the uppermost part of the style channel (c), here filled with the fragments of cell walls, t – small celled tissue as in Fig. 19.

Fig. 21. The stigma with pollen grains, general view, (SEM, x 150).

Fig. 22. As 21, but magnified, note multiple pollen grains among the papillae; visible fragments of pellicula, (SEM, x 750).

Fig. 23. As 21 and 22 but more magnified, visible thorny trichomes, (SEM, x 1500).

Fig. 24. Germinated pollen grain on the stigma, (SEM, x 3000).

more rarely were encountered the ramified simple or glandular trichomes.

4. Large, very ramified, dendritic hairs, well visible with the naked eye, without glandular structures (Fig. 25). These hairs were found mainly at the lower part of the petals closing partly the access to the ovary (Fig. 27). Usually together with them but a little more distally the glandular hairs of the type "3" were found.

The anther of tomatillo was two-lobed and tetrasporangiate (Fig. 16). In its connective there was one vascular bundle. In each lobe, the longitudinal septum between microsporangia was visible, built of irregular, parenchyma cells already degenerating in the stage of development shown in Fig. 16. The endothecium was three layer thick near the connective and reduced to one layer close to the dehiscence fissure. The epidermal cells have been smaller and smaller and more flattened approaching the dehiscence fissure. However, the 2 to 3 cells of epidermis close to the fissure, on each side of it, were very large and sometimes had been divided periclinally. The cells just closing the fissure were very reduced but with well visible nuclei (Fig. 17).

The pollen grain was spherical, three-colpate (Fig. 18). The apertures were elongated. In the center of each of them the apex of pollen tube was protruding. The exine showed granulated surface.

The gynoecium was composed of three carpels (compare Dyki et al. 1997). The style was roundish in cross section, with a hollow channel inside, triangular in cross-section (Fig. 19). There were usually six vascular bundles supplying it (sometimes two of them were joined). The walls of the channel were covered by a stratum of small-celled tissue with dense cytoplasm. The cells visible on the surface of the style were elongated parallel to its main axis (Fig. 20).

The stigma was triangle-like, as seen from above, concave with a deep cavity in the center tapered with the exudate (Figs 20 and 21). The cells of the stigma formed high finger-like papillae among which the pollen grains were captured

Fig. 25. The large ramified, dendritic trichomes found on the basal part of the adaxial surface of the petal (see arrow in Fig. 26).

Fig. 26. The cross section of fully open tomatillo flower (a scheme). The arrow indicates where the long ramified hairs are situated. Only one stamen is shown, (x 2)

Fig. 27. The hairs at the margin of the petal (Pt), the leaf (Lf) and the sepal (Sp); A – the apex, (x 300, the bar = 50 μ m.)

(Figs 22, 23). The stigma was of wet type. The pellicula covered the stigma surface and was visible among the papillae (Figs 22-23), the pollen tubes were penetrating the pellicula (Fig. 24). Thorn-like trichomes of different shape might be sometimes found on the stigma (Fig. 23).

DISCUSSION

Leaf structure of tomatillo was similar to that of tobacco or potato in having, generally, one palisade parenchyma layer (Esau 1965, Malinowski 1980). There was observed, however one peculiarity of tomatillo leaf – the spongy parenchyma cells situated just below the palisade parenchyma were very large and many of them contained large druses and individual crystals with the shape typical for calcium oxalate (see Esau 1965). Although these cells, were closely packed and could eventually hamper the access of the air to the palisade parenchyma from beneath, nevertheless, the palisade parenchyma in tomatillo may be aerated by the stomata in the adaxial epidermis.

The ordinary and glandular trichomes of tomatillo leaf were very similar to those of cultivated potato (McCauley and Evert 1988) and of wild potatoes (Gibson 1971). More dense occurrence of trichomes along the veins was also observed in other species of plants (McCauley and Evert 1988). The short, simple, unicellular trichomes on the margin of tomatillo leaf were very similar to those found by Gibson (1971) on the margin of potato *S. tuberosum* leaf. We have never observed the accumulation of secretory product in a "bag" between the cell wall and the cuticle in glandular hairs as have been found by Afolayan and Meyer (1995) in *Helichrysum*, and have been also described by Fahn (1988) and Bosabalidis and Exarchou (1995), however, for definitive proof that the "bag" is not formed the transmission electron microscope should be used in the future.

The anatomical structure of the calyx have presented the typical structure since its mesophyl was not differentiated into the palisade and spongy stratum (Esau 1965). The numerous cells which showed the arrangement in pairs or tetrads, typical for freshly divided cells agree with the fact that tomatillo calyx is intensively growing during the flowering and afterwards during fruit growth to form the fruit envelope. The other peculiarity of tomatillo calyx were the stomata on the hills or columns built of many cells. Similar structures were encountered in *Cucurbita*, and *Luffa* leaves and stems and in some other plants from other families (Metcalf and Chalk 1979). It is difficult to find any physiological reason for such structures. The adaxial surface of the calyx in the half grown fruits was covered by a deposit of a wax-like substance sensible even by touch. It may be supposed that this wax-like layer may serve as a lubrication when the fruit is emerging from calyx envelope and finally disrupts it. The trichomes at the margin of the sepal were much smaller than those on the margin of the petal and were almost all of ordinary character. This may be caused by the fact that in a fully developed flower (in which the sepals and petals were compared) the petals have almost finished their growth whereas the sepals are just at the beginning of their development and their trichomes might be in much earlier stage of development.

The very delicate anatomical structure of tomatillo petal agrees with the fact that the flowers of this plant are very undurable – their petals last only one to few days after being developed and they wilt. Taking into account that the petal mesophyl is so loose and delicate, the epidermis seems to play an important additional role as a "mechanical" tissue contributing to petal integrity. The undulate surface of the petal epidermis: very convex external walls and the papillae found on almost each cell on the adaxial side play probably a role in increasing the attractiveness of the flower for the insects. Smooth surface of the petal would produce the effect of glittering which probably would not permit good recognition

of the color, whereas undulate structure reflects the light in all directions giving the effect of deep coloration and prevents glittering. The question remains if glittering would be indeed an interfering factor in color perception for insects. Kay et al. (1981) have found only 5% of species belonging to different families, which had flower petals with flat epidermis (but frequently with surface striation) and 79% species with papillate or lenticular petal surface. The remaining species showed the depressions in cell surface.

The different glandular hairs near the basis of the petal may produce nectar or aromatic substances but this was not investigated by us in this work. The large, highly ramified, dendritic hairs which partly closed the access to the ovary and receptacle might protect these parts from excessive drying and other unfavorable influences.

The stamens of tomatillo were typical for most of the angiosperms. They had filament and were tetrasporangiate (see Bhandari 1984). The wall of a mature anther comprised the epidermis and endothecium. The endothecium was multi-layered like in *Nicotiana tabacum* and *N. glutinosa* (Jose and Singh 1968).

The pollen grain of tomatillo had similar shape to that of tobacco (*Nicotiana tabacum*) presented by Bedinger (1992). Only the sculpture of the exine differed: in tobacco it was densely striated and in tomatillo granulated and with fine spines.

The channel inside the tomatillo style was stuffed by a stratum of the tissue built of small cells containing dense cytoplasm. They were probably of glandular character. Such tissue and the channel serves usually as a way for pollen tube growth. Similar structure of the style was observed in *Amaryllidaceae*, especially in *Sternbergia lutea* (Ciampolini et al. 1990). The style of *Lycopersicon peruviana* and *Nicotiana sylvestris* (Cresti et al. 1976, Kandasamy and Kristen 1987) were of solid type (without the channel), although in *N. sylvestris* the internal tissue of the style was very loose and showed large, longitudinally arranged cavities. In several other plants recently investigated, the wet papillate stigma was accompanied by solid structure of the style as in *Vitis vinifera* (Ciampolini et al. 1996), or by half solid style as in *Hacquetia epipactis* – *Apiaceae* (Weber and Forsch 1995).

The stigma of tomatillo resembled those of other Solanaceae as being of wet type and showing papillae emerging from pellicula (Heslop-Harrison and Shivanna 1977, Kandasamy and Kristen 1987). However, the stigma of wild tomato (*Lycopersicon chilense*) was very convex and roundish (Dyki and Kozik 1995), whereas that of tomatillo was flattened at the top and showed the central depression plugged with pellicula or glandular exudates. The thorny, ramified trichomes found sometimes on tomatillo stigma resemble in some way those on the leaf of *Fuertesia domingensis* (Poston and Nowicke 1993). The wet papillate stigma occurs in many species of plants belonging to different families (Heslop-Harrison and Shivanna 1977).

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BUDOWA ANATOMICZNA I MIKROMORFOLOGIA
POWIERZCHNI LIŚCIA I KWIATU MIECHUNKI POMIDOROWEJ
(*PHYSALIS IXOCARPA* BROT., SOLANACEAE)

STRESZCZENIE

Miechunka pomidorowa (*Physalis ixocarpa* Brot.) jest rośliną niedawno wprowadzoną do uprawy w Polsce. Jej budowę badano przy pomocy mikroskopu świetlnego i skaningowego. Dojrzały liść miechunki ma jedną warstwę miękiszu palisadowego. Najwyższe 1-2 warstwy miękiszu gąbczastego są zbudowane z komórek większych niż pozostałe, ściśle ułożonych, zawierających duże druzy. Pozostałe komórki tego miękiszu mają liczne wybrzuszenia łączące je z innymi komórkami. Osobliwością zewnętrznej (abaksjalnej) powierzchni działek kielicha są aparaty szparkowe położone na wzgórkach (kolumnach) zbudowanych z wielu komórek. Płatki korony mają bardzo luźny miękisz oraz epidermę z komórkami o zewnętrznej ścianie bardzo wypukłej z brodawką na szczycie. Taka mikrostruktura powierzchni rozprasza światło i zapobiega błyszczeniu co może sprzyjać percepcji barwy przez owady. Opisano kilka typów włosków: zwykłych i gruczołowych występujących na powierzchni liści, działek i płatków. Duże, silnie rozgałęzione drzewiaste włoski w pobliżu nasady płatków prawdopodobnie chronią zalążnię przed nadmiernym wysychaniem. Ziar- no pyłku jest kuliste, trójszczelinowe z wystającymi wierzchołkami łagiewek pyłkowych. Egzyna ma powie- rzchnię gruzelkowatą. Słupek ma pusty kanał w środku. Znamię słupka jest typu mokrego. Jego komórki tworzą dość długie brodawki.

SŁOWA KLUCZOWE: anatomia liścia, anatomia kwiatu, mikromorfologia powierzchni, włoski, ziarna pyłku, *Physalis ixocarpa*.