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RESEARCH ARTICLE

Structural-functional signs of *Typha angustifolia* leaves plasticity depending on the growth conditions

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Abstract

The results of the study of leaf anatomy and leaf epidermal ultrastructure of the heliophytic plant *Typha angustifolia* L. (Typhaceae), which grew in natural conditions: in the water on the bank of the Venetian Strait of the Dnipro River (Kyiv) and on land near the Strait, using light microscopy and scanning electron microscopy are presented. The common and distinctive features of the anatomical signs and the ultrastructure of epidermal cells of *T. angustifolia* leaves in the phase of vegetative growth of plants were revealed. The anatomical and morphological characteristics of leaves of two ecotypes of *T. angustifolia* that grew in water and on the terrestrial soil did not differ; the type of mesophyll and the presence of two zones in the epidermis (the zone of convex vault and stomata zone) is stable features for this species. Differences in the size of the leaf blade, the density of stomata, and the density of wax coating on the surface of epidermal cells of the convex vault zone, and also the presence of amorphous silicon in the cell walls of the epidermis are adaptive, and plastic traits that vary depending on the conditions of cattail growth. Besides, scanning electron microscopy of the leaf epidermis of cattail grown in water and on terrestrial soil revealed that growth in water causes the formation of stomata that are deepened into the epidermis, as well as the presence of closed stomata on the lower epidermis, while in the leaves of terrestrial cattail, all stomata were open and located at the same level as the regular epidermal cells. It is assumed that the deepening of stomata into the epidermis contributes to the optimal water balance of leaves under wave action of Strait and high humidity around the leaves of air-water cattail. The obtained results are discussed as a manifestation of phenotypic plasticity and the possible use of epidermal wax as an adaptive marker of heliophytes for growth in different water supply conditions.

Keywords: *Typha angustifolia*, leaves, anatomic signs, epidermis ultrastructure, wax

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Introduction

The problem of plant resistance and adaptation to adverse environmental changes not only remains one of the primary problems of theoretical and experimental biology but is also significantly exacerbated by the increasing anthropogenic load on the biosphere and the forecasts of global climate change, which threaten to increase air temperature, drought, and floods. Some of these factors are the intensity of sunlight, flooding, and changes in soil moisture, which are characterized by a combination of changes in the water balance of plant organs, impaired oxygen respiration in the root system, and as a result, inhibition of aerobic processes, impaired absorption of ions from the soil, lack of nutrients, changes in metabolic transport, and restrictions on plant growth and development (Jackson & Armstrong, 1999; Jackson, 2008; Pennisi, 2008; Malavasi et al., 2016). Despite this, plants develop mechanisms of adaptation to unfavorable conditions at different levels of organization (from morphological to genetic) that help them to adapt to the changed environment. It is believed that phenotypic plasticity is the basis for the survival and conservation of populations, as well as a key element of evolution and ecological relationships of species in habitats (Kordyum, 2012; Dubyna & Kordyum, 2015; Kordyum & Dubyna, 2019).

A convenient natural model for studying the adaptive capacity of plants to both natural flooding and growth under conditions of varying sunlight and moderate soil drought may be species that have naturally adapted to grow in contrasting environmental conditions. Such a species is the narrow-leave cattail *Typha angustifolia* L., a closely related monoecious wetland plant native to Europe, common in the temperate zone of the Northern Hemisphere. Typha angustifolia belongs to the Typhaceae family; it is a heliophyte, a light-loving herbaceous perennial aquatic plant (0.8–1.5 m tall). The leaf arrangement is alternate; the stem is covered with leaves up to the top. The stem of the cattail is erect, round, thick, glabrous, and smooth (Chopyk et al., 1983). The leaves are linear-lanceolate, flattened. In aquatic plants, the leaves are straight, while in terrestrial plants, the leaves can be either straight or slightly curled inwards.

Because of their widespread distribution and prevalence, *Typha* communities form an important and widespread type of wetland that provides natural protection against extreme flooding, conserving freshwater and improving its quality. They provide habitat for many species of invertebrates and vertebrates, providing spawning grounds for fish and amphibians, and offering birds hiding and nesting places (Mitsch & Gosselink, 2000; Bobbink et al., 2006; Heinz, 2010). *Typha* species are among the preferred plants in artificially created wetlands due to their high carbon dioxide and nutrient uptake capacity and ability to purify water even in heavy metal pollution (Saygdeger et al., 2004; Bobbink et al., 2006). It is known that signs of phenotypic plasticity of higher plants to changes in soil moisture include changes in the anatomy of organs and changes in the ultrastructure of the leaf epidermis involved in water and gas transport (Nedukha, 2022). We hypothesized that similar changes could be observed in a cattail species growing in contrasting conditions: water and land. Our study aimed to investigate the anatomical features of the leaves of aquatic and dryland cattail plants and to study the ultrastructure of the leaf blade surface.

Material and methods

The object of the study was the leaves of the narrow-leave cattail *Typha angustifolia* (family Typhaceae) growing in water on the shore of the Venetian Gulf (left bank of the Dnipro River, in the Kyiv area) and on terrestrial soil about 3–4 m from the shore (Fig. 1). Narrow-leave cattail plants grew in water at a depth of 40-50 cm along the shore of the Venetian Gulf. Terrestrial plants grew on semi-sandy terrestrial soil near the shore. Material for the study was collected in the vegetative growth phase in mid-May. The water temperature on the collection day was +14 °C, and the air temperature was +16 °C.

The first leaves from seven plants of each cattail ecotype were used for microscopic studies. The material for cytological studies was fixed in the field. Cuttings from the broadest part of the leaf blades were selected for experiments. Leaves that had completed growth by stretching were used

Figure 1. The general appearance of *Typha angustifolia* plants, which grew in water (**A**) and terrestrial soil (**B**). Comparison of *T. angustifolia* leaves (**C**) of the plant grown in water on bank (**white arrow**) and leaves of terrestrial plant (**black arrows**).

for the study. Samples were fixed for light and electron microscopy with a mixture of 2% glutaraldehyde and 2% paraformaldehyde (1:1, v/v) in 1 M phosphate buffer, pH 7.2, directly on the bank, and delivered to the laboratory, where they were washed with buffer, dehydrated, and embedded in an epoxy resin mixture (epon–araldite) according to the generally accepted method (Bücking & Heyser, 2000). Sections of 10 μm thickness were made on an RMC MT-XL ultramicrotome (USA), stained with an aqueous solution of methyl red, crystal violet-lactone, and silver amino chromate according to the protocol (Dayanandan et al., 1983) and examined under an NF light microscope (Carl Zeiss, Germany). For scanning electron microscopy, the fixed material in the aldehyde mixture was dehydrated and dried according to the protocol (Bücking & Heyser, 2000). Then, the leaf blade samples were mounted on tables, sputtered with gold, and examined in a scanning electron microscope (JSM 6060 LA) at 30 kV. Statistical processing of stomatal density and cell size values was performed using Origin 6.1 software and Student's *t*-test ($P \leq 0.05$).

Leaves from seven plants were used to determine the linear dimensions of the leaves. Linear cell size was determined on sections from three water cattail leaves and three terrestrial cattail leaves. From each sample, 30–40 epidermal cells and 40-50 mesophyll cells were taken. A standard biochemical method based on drying the samples in a thermostat at + 95 °C until the weight is constant was used to determine the relative water content in the leaves. The obtained cytological and biochemical data were processed statistically.

To determine the soil moisture content on which the cattail plants grew, soil samples were taken at a depth of approximately 20 cm from the surface. The soil samples were dried in a thermostat at a temperature of +105 °C to a constant weight. It was found that the moisture content of the soil on which the aquatic cattail plants grew was 81 ± 2.3%, while the moisture content of the soil on which the terrestrial cattail plants grew was 57.3 ± 1.9%.

Results

The leaves of aquatic and terrestrial *T. angustifolia* plants were characterized by a linear-lanceolate shape (Fig. 1), longitudinal venation, smooth upper surface, and a central vein distinguished on the lower surface. The leaves of cattail growing in water were smaller than those of cattail growing on terrestrial soil. The average size of the cattail leaves grown in water was 43.7 ± 5.9 cm along the long axis and 2.1 ± 0.3 cm along the short axis. Leaves of terrestrial cattail were 54.3 ± 3.7 cm along the long axis and 3.2 ± 0.4 cm along the short axis. The water content in the leaves of water cattail was 64.7 ± 0.5%, and in the leaves of terrestrial cattail – 47.2 ± 0.7%.

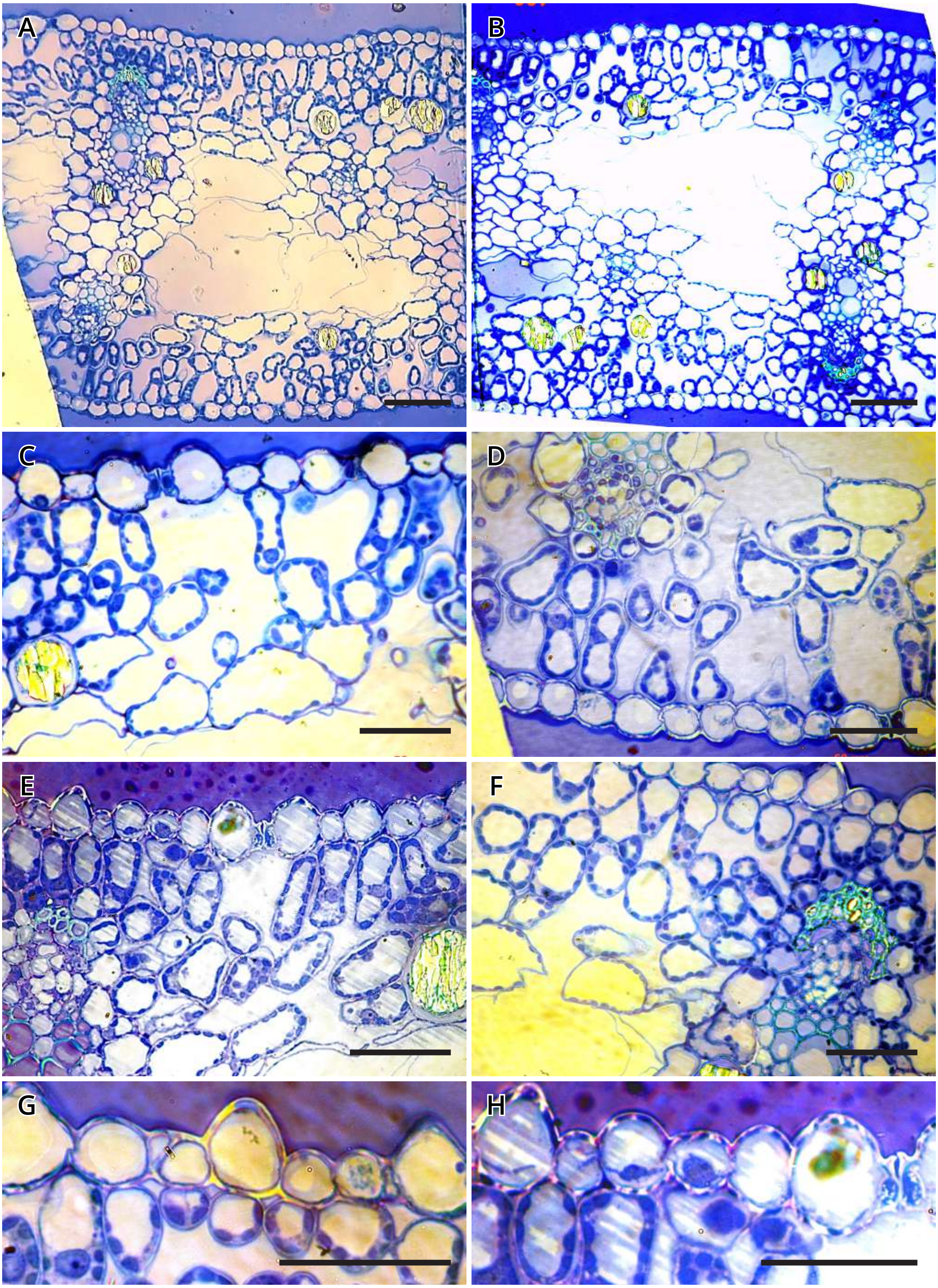

Figure 2. Transverse sections of the middle part of the leaf blades of *Typha angustifolia,* which grew in the water (**A, C, D, G**) and terrestrial plants (**B, E, F, H**). Scale bars: **A, B** = 100 μm; **C–H** = 50 μm.

Anatomical structure of leaves (Fig. 2)

Leaves of T. angustifolia plants, which grew in the water

The structure of the leaves is isolateral type (Fig. 2 A). The leaves were characterized by the presence of collateral conductive bundles, which, together with mesophyll cells, divided the leaf blade into areas in the center of which a large aerenchyma was formed. The aerenchyma was formed by the lysis of the palisade and spongy mesophyll (Fig. 2 C, D).

The average thickness of the leaf blade was 600±21 µm. The adaxial epidermis is characterized by rounded cells of different sizes; the cells surrounding the deepened stomata were larger than regular epidermal cells. The height of large epidermal cells was 24.6±2.1 µm, the height of small epidermal cells was 13±1.2 µm, while the width of large cells was 25±2.1 µm and small cells was 12.7±1.3 µm, respectively. The palisade parenchyma cells were elongated (Fig. 2 C); their size was 50±3.7 × 15±2.1 µm. The average number of chloroplasts per mesophyll cell was 12.3±1.5. The cells of the spongy parenchyma varied in shape from elongated polygonal to rounded (Fig. 2 D). The size of these cells ranged from 45±3.7 × 21±2.1 µm to 13±1.7 µm (diameter, rounded cells). The spongy parenchyma cells surrounding the upper and lower conducting bundles form a continuous 'partition' between the large air cavities (lysogenic aerenchyma). The lower epidermis is similar in structure and cell size to the cells of the upper epidermis (Fig. 2 D). The height of the large cells of the lower epidermis was 23.1±2.3 µm, the height of the small epidermal cells was 12.4±1.2 µm, while the width of these cells was 25.2±2.1 µm and 12.1±1.3 µm, respectively.

Leaves of terrestrial T. angustifolia plants

The anatomical and morphological characteristics of terrestrial cattail plants were similar to those that grew in water; the structure of the leaf blade was also isolateral (Fig. 2 B, E, F). The average thickness of the leaf blade was 623±32 µm. The shape of the epidermal and mesophyll cells was similar to that of the leaves of air-water cattail plants. The average size of large cells (height × width) of the upper epidermis was 23.3±2.2 × 24±2.5 µm, the size of small cells was 12.3±1.2 × 13±1.9 µm; of the lower epidermis – 21.3±2.1 × 20±2. 1 µm, and small cells – 11.3±1.2 × 12±1.9 µm; palisade mesophyll cells –51±3.3 × 13±2.0 µm and spongy mesophyll cells – from 42±3.7 × 21±0.9 to 10±1.3 (for rounded cells) µm, respectively. The average number of chloroplasts per section of mesophyll cells was 13.4±2.5.

It should be noted that the mesophyll cells and cells of the conducting bundles in the leaves of two cattail ecotypes on the sections were blue stained. In contrast, epidermal cells, especially of the adaxial surface around the perimeter of all epidermal cell walls, were stained in bright yellow hot color with a red tint, which is visible at high magnification of the microscope after staining the sections with an aqueous solution of methyl red, crystalline violet lactone and silver amino chromate (Fig. 2 G, H). Similar staining could be observed occasionally in the palisade parenchyma cell walls in contact with the upper epidermis in the leaves of terrestrial cattail (Fig. 2 E).

Microstructure of *T. angustifolia* leaves epidermal surface (Figs. 3, 4)

The study of the ultrastructure of the surface of leaves of aquatic and terrestrial plants of narrow-leave cattail revealed the presence of two zones of different structures on the adaxial and abaxial surfaces: the convex vault zone and the stomatal zone (Figs. 3, 4). Differences in the ultrastructure of the surface of air-water and terrestrial plants were manifested in the density of stomata, the presence and structure of waxy inclusions on the cell surface, as well as in the deepening of stomata in the epidermis of water cattail leaves.

The leaf epidermis of T. angustifolia plants, which grew in the water (Fig. 3)

Adaxial surface (Fig. 3 A–C). The width of the convex vault zone ranged from 22±2.1 to 53±4.1 µm; the width of the stomata zone ranged from 68±3.7 to 82±7.4 µm, respectively. On the surface of the convex vault zone of the upper epidermis, individual cells were distinguished, the anticlinal walls of which protruded above the periclinal walls, and the thickness of the anticlinal walls was ca. 5 µm. Trichomes and waxy inclusions were absent on the surface of epidermal cells of the convex vault zone. Meanwhile, in the stomatal zone, the surface of ordinary epidermal cells was covered with waxy structures of various shapes (Fig. 3 B, C):

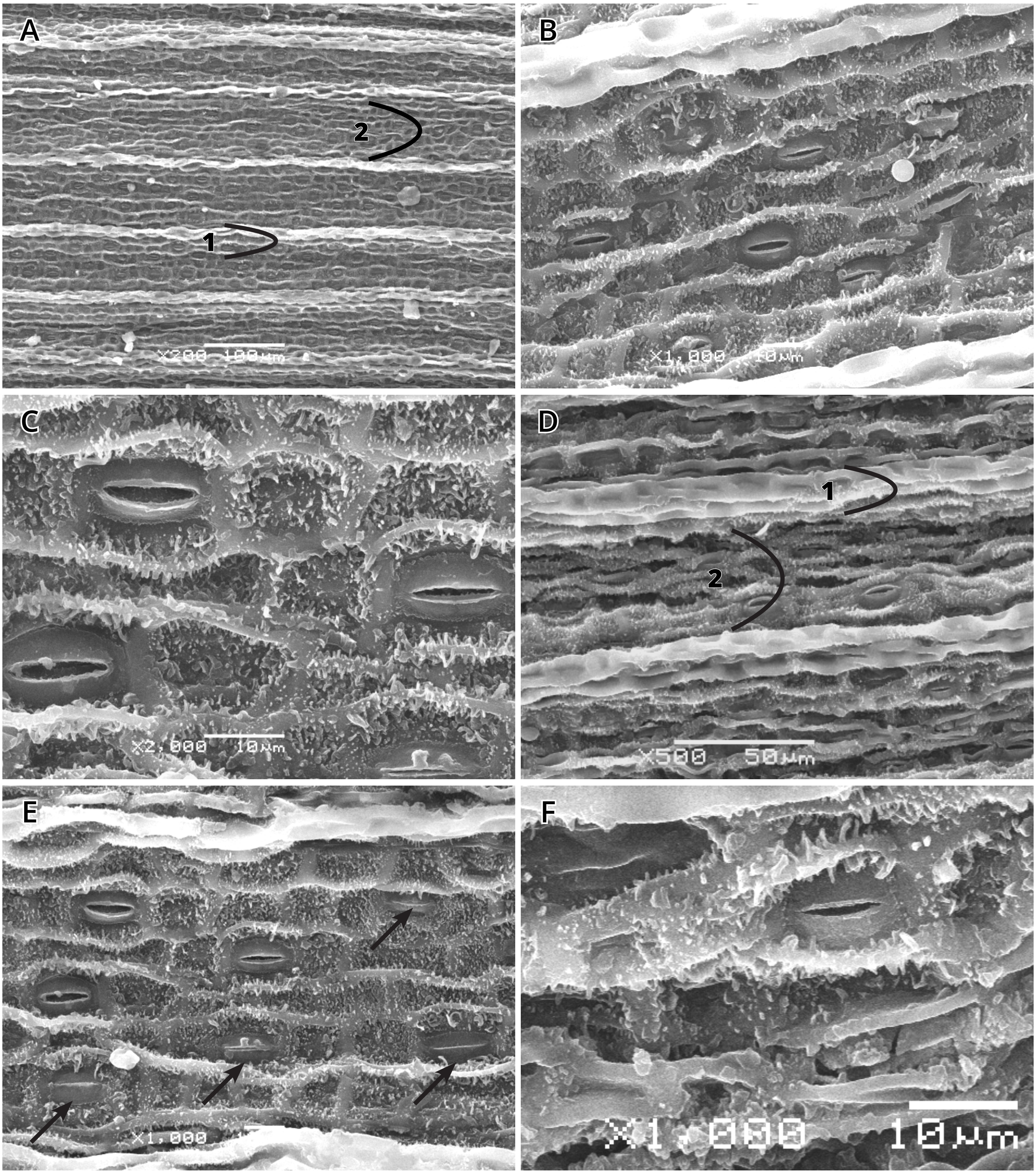

Figure 3. The ultrastructure of the adaxial (**A–C**) and abaxial (**D–F**) leaf surfaces of *Typha angustifolia* plants, which grew in the water. The **black curved lines** (**A & D**) indicate: **1** – convex vault zone; **2** – stomata zone. Closed stomata are indicated by **black arrows** (**E**).

needle-shaped, drop-shaped, or triangular. Wax inclusions were of different sizes (1 to 3 µm along the long axis). Stomatal density was 534 ± 17 per mm^2 area. Stomata are elongated and deepened. Epidermal cells located around the stomata are raised. The surface of the stomatal guard cells is smooth, without wax. Stomata size was 18 ± 1.1 µm along the long axis and 14 ± 1.7 µm along the short axis.

Abaxial surface (Fig. 3 D–F). It is also characterized by the presence of two structural zones, similar to those on the upper surface of the leaf in terms of the ultrastructure of epidermal cells and the

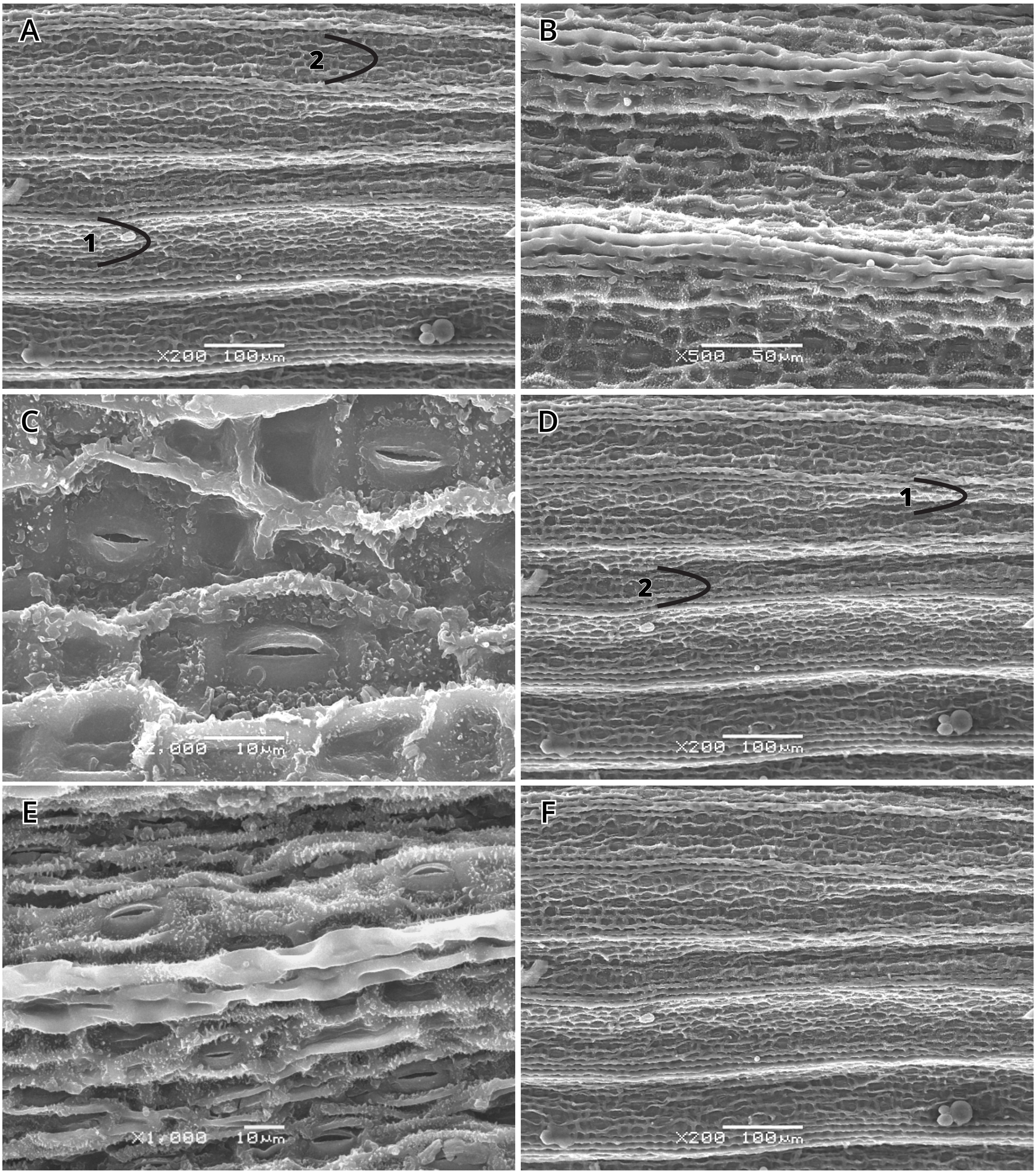

Figure 4. The ultrastructure of the adaxial (**A–C**) and abaxial (**D–F**) leaf surfaces of terrestrial *Typha angustifolia* plants. The **black curved lines** (**A & D**) indicate: **1** – convex vault zone; **2** – stomata zone.

structure of stomatal guard cells. The only difference was a decrease in the width of the convex vault zone to 21 ± 2.0 µm. The density of stomata on the lower epidermis was 610 ± 23 per mm^2; closed stomata were observed along with open stomata (Fig. 3 E; lower row of closed stomata cells indicated by arrows).

The leaf epidermis of terrestrial T. angustifolia plants (Fig. 4)

Adaxial surface. The presence of two structurally distinct zones is also characteristic of terrestrial cattail leaves (Fig. 4). The surface of the convex vault zone of the epidermis is covered with wax structures. The width of the convex vault zone varies from 45.2 ± 4.1 to 55.0 ± 5.7 µm. On the surface of the convex vault, anticlinal walls are visible, similar to those of water cattail, with a width of 4 to 6 µm. The anticlinal protruding and recessed periclinal walls are densely covered with wax structures (plaque) of various shapes: round, triangular, or square. Wax structures can also be seen on the periphery of stomatal guard cells (Fig. 4 C). The stomata are elongated, with a density of 414 ± 12 per mm^2 area.

Abaxial surface. Abaxial epidermis is characterized by the presence of two zones similar to those on the upper epidermis: the convex vault zone and stomata zones (Fig. 4 D–F). The average width of the stomata zone ranges from 50 ± 3.7 to 67 ± 7.1 µm, and the width of the convex vault zone is from 23 ± 3.7 to 50 ± 4.1 µm, with arrow-shaped (or triangular) wax structures clearly visible on the surface of the tubercle zone. The surfaces of the stomatal guard cells, which are not deepened but are almost at the level of the regular epidermal cells, are encrusted with wax structures (Fig. 4 E, F). The density of stomata on the lower epidermis is 458 ± 23 per mm^2 of area.

Discussion

Thus, our studies of the anatomical and morphological characteristics of the leaves of aquatic and terrestrial cattail *T. angustifolia* showed that, regardless of the place of growth of cattail, the leaves were characterized by a similar anatomical structure with an amphistomatic type of structure and large aerenchyma cavities. A similar anatomical structure of leaves is also characteristic for other Typhaceae, including *T. latifolia* L. growing in Eurasia, namely, an amphistomatic type of leaf blades with sclerenchymal conductive bundles that connect palisade and spongy parenchyma, forming partitions between large aerenchymal formations (Henry, 2003).

Despite the identity of the anatomical structure of the studied objects, we found differences in the size of leaf blades of aquatic and terrestrial cattail plants: significantly larger leaf sizes of terrestrial cattails than those in plants grown in the water. There may be several reasons for the differences in leaf size: lack of nutrients for water cattail, different cell cycle rates, different ploidy, and differences in population density. The growth of higher plants in water is known to be characterized by both partial hypoxia and a particular nutrient limitation, which is typical for different grass populations (Insausti et al., 2001). We also do not exclude the possibility that the aquatic and terrestrial cattail plants that we studied are characterized by different ploidy, which is known to affect morphological traits; in particular, such a relationship has been established for reed leaves (Clevering & Lissner, 1999; Paucă-Comănescu et al., 1999; Hansen et al., 2007). Researchers have shown that the lower the ploidy, the smaller the cell size (Hansen et al., 2007). This relationship between ploidy level and morphology is generally biological, as a relevant and general effect of polyploidy is increased cell size. However, polyploidy does not always lead to an overall increase in plant size, as a general effect of polyploidy can also be a decrease in the number of cell divisions during development (Stebbins, 1971).

Particularly noteworthy are the data of researchers who studied the effect of *T. angustifolia* and *T. domingensis* Pers. population density on the anatomical and physiological characteristics of these species (Corrêa et al., 2015). The authors showed that an increased growth rate characterizes plants from populations with high cattail density. Corrêa et al. (2015) attribute this phenomenon to lower apoplastic barriers in the roots and to an increased ability to absorb nutrients, as well as to a particular root/shoot size ratio, compared to plants with low density (less than 50 % of the colonizing capacity). Given these data, we assume that the morphological structure of the leaves of the two cattail populations we studied was also influenced by the density of these plants: the land-based population with high density had larger leaf sizes than the cattail plants growing at low density (in water). Thus, the complex structural, physiological, and genetic mechanisms of leaf plasticity of narrow-leave cattail plants growing in the Kyiv area require further investigation.

In addition to the differences mentioned above, we also found certain differences in the stain of the cell walls of mesophyll and epidermal tissues of the studied samples of narrow-leave cattail. The walls of epidermal tissues, especially the adaxial epidermis, acquired a hot yellow color with a red tint, regardless of the place of growth of the species. The mesophyll walls adjacent to the adaxial epidermal cells in the leaves of the terrestrial cattail also had a similar color (Fig. 2 E, H), while the mesophyll walls of the leaves of aquatic cattail plants were blue. The peculiarity of this phenomenon is the physical property of the dye – methyl red, a crystalline violet lactone, which, when combined with silicon ions (SiOH), dyes amorphous silicon in cells in such bright color (Dayanandan et al., 1983; Guerriero et al., 2020). Based on the above data, we assume that the epidermal walls of cattail leaves contain amorphous silicon, similar to those in the leaves of many plant species, including leaves of rice, bamboo, and other species (Dayanandan et al., 1983; Blecher et al., 2012; Guerriero et al., 2020). Obviously, the presence of amorphous silicon in the walls of the epidermis and mesophyll of narrow-leave cattail leaves is a structural and functional feature that determines the optimal water and osmotic balance of the leaves.

Our data on the ultrastructure of the leaf surface of aquatic and terrestrial cattails revealed both common and different features. The common feature was the presence of two structurally different zones (stomatal and convex vault) in the epidermis. Whereas the differences were manifested in the density of stomata, the increase of wax coating on the surface of epidermal cells in the convex vault zone and the stomatal zone, as well as the presence of wax on the periphery of stomatal guard cells in the leaves of dry cattail. The presence of two zones in the leaf epidermis is also characteristic of other species of this family, in particular, *T. domingensis* (Cruz et al., 2019) and *T. angustifolia*, which grew in Brazil (Corrêa et al., 2015).

We also discovered a phenomenon - almost half of the stomata on the lower epidermis of the water cattail were closed entirely. These data require an explanation. On the one hand, it is known that stomatal functions are associated not only with the regulation of water balance (transpiration and cell osmotic pressure), but also with CO_2 uptake for photosynthesis (Boyer et al., 1997; Lawson & Blatt, 2014; Roche, 2015). Hence, stomatal conductance is a key physiological parameter that regulates plant growth and development under normal and stress conditions (Hetherington & Woodward, 2003; Hasanuzzaman et al., 2023). Aquatic cattail plants with higher stomatal conductance (on the upper epidermis) are characterized by a high rate of CO_2 assimilation. The presence of a large proportion of closed stomata on the lower epidermis of aquatic cattail leaves can be explained by two reasons. First, some stomata are temporarily inoperative, as natural conditions can induce surface-specific stomatal closure (Richardson et al., 2017). The second reason is the complete non-functionality of a part of stomata in water cattail, similar to that described for the leaves of aquatic plants, in particular *Salvinia herzogii* de la Sota, *Lemna minor* L. (Ziegler, 1987; de la Sota et al., 1990; Shtein et al., 2017), *Nymphaea violacea* Lehm. and others (Kaul, 1976; Ziegler, 1987), in which gas exchange occurs only through the upper surface of the leaves. In addition, the closure of stomata on the lower epidermis of water cattail may be associated with the fact that the lower surface can be affected by the water environment and waves, and this surface can also be in contact with the surrounding aquatic microflora and numerous algae (Tyree, & Cheung, 1977; Nedukha, 2011).

When studying the ultrastructure of the epidermis of cattail leaves, we found an increase in the content and density of wax inclusions on the surface of the epidermal walls. It is known that the wax formed on the outer surface of epidermal cells inhibits transpiration and can absorb and/or reflect sunlight (Kolattukudy, 1981; Schönherr, 1982; Kerstiens, 1996, 2006). The wax formed on the cell surface, together with cuticular wax, is one of the barriers to water evaporation and an inhibitor of the transport of small water molecules both from the epidermis and their transport into the cells (Hauke & Schreiber, 1998; Barthlott et al., 2017). Based on this literature and our scanning electron microscopy data, we can assume that the ‘exit’ of cattail plants from water to terrestrial soil (to land) causes an increase in the formation of wax in the leaf epidermis, and this is a manifestation of the phenotypic plasticity of the plants of the studied species. We believe that wax structures on the surface of epidermal cells can be a marker of changes (or decreases) in water transport in plant leaves. Using these traits in breeding and/or genetic studies will allow researchers to select species that can adapt to environmental stresses, such as drought or changes in plant water supply.

Conclusions

The anatomical and morphological characteristics of leaves of two ecotypes of *Typha angustifolia* grown in water and on the terrestrial soil did not differ: the type of mesophyll and the presence of two zones in the epidermis: the zone of convex vault and stomata zone is stable features for this species. Differences in the density of stomata and the density of wax coating on the surface of epidermal cells indicated the phenotypic plasticity of the species and the modification of leaf structure depending on the growth conditions, particularly soil moisture. Scanning electron microscopy of the leaf epidermis of cattail grown in water and on terrestrial soil revealed that growth in the water causes the formation of stomata that are deepened into the epidermis, as well as the presence of closed stomata on the lower epidermis, while in the leaves of terrestrial cattail, all stomata were open and located at the same level as the regular epidermal cells. It is assumed that the deepening of stomata into the epidermis contributes to the optimal water balance of leaves under conditions of wave action and high humidity around the leaves of the water cattail.

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Структурно-функціональні ознаки пластичності листків *Typha angustifolia* в залежності від умов зростання

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Наведено результати дослідження анатомії та ультраструктури епідермісу листків геліофітної рослини *Typha angustifolia* L. (Typhaceae), яка зростала в природних умовах: у воді на березі Венеціанської протоки р. Дніпро (м. Київ) та на суші поблизу берега протоки, методами світлової мікроскопії та скануючої електронної мікроскопії. Виявлено спільні та відмінні риси анатомічних ознак та ультраструктури клітин епідермісу листків *T. angustifolia* у фазі вегетативного росту рослин. Анатомо-морфологічні ознаки листків двох екотипів *T. angustifolia*, що зростали у воді та на суходолі, не відрізнялися; тип мезофілу та наявність двох зон в епідермісі (зона опуклого склепіння та зона продихів) були стабільними ознаками для цього виду. Відмінності в розмірах листкової пластинки, щільності продихів та щільності воскового нальоту на поверхні клітин епідермісу зони випуклого склепіння, а також наявність аморфного кремнію в клітинних стінках епідермісу є адаптивно-пластичними ознаками, які змінюються залежно від умов зростання рогозу. Крім того, скануюча електронна мікроскопія епідермісу листків рогозу, вирощеного у воді та на суходолі, показала, що зростання рослини у воді спричиняє формування продихів, заглиблених в епідерміс, а також наявність закритих продихів на нижньому епідермісі, тоді як у листках наземного рогозу всі продихи відкриті і розташовані на одному рівні з основними клітинами епідермісу. Припускається, що заглиблення продихів в епідерміс сприяє оптимальному водному балансу листків в умовах хвильової дії затоки та підвищеної вологості навколо листків повітряно-водного рогозу. Отримані результати обговорюються як прояв не тільки фенотипової пластичності, але й можливого використання епідермального воску як адаптивного маркера геліофітів для зростання в різних умовах водозабезпечення.

Ключові слова: *Typha angustifolia*, листки, анатомічні ознаки, ультраструктура епідермісу, віск