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RESEARCH ARTICLE

The role of silicon ions in the resistance of *Typha angustifolia* to reduced soil moisture

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Abstract

The results of the study of the localization and content of silicon in the leaves of narrow-leaved cattail (*Typha angustifolia*) plants, which grew in natural conditions on the shore of the Venetian Bay (in the Kyiv area), are presented: in water and on land. To determine the localization and content of silicon in the leaves, cytochemical and ultrastructural methods were used. Leaves were taken for the study in the vegetative growth phase. The presence and localization of silicon ions were studied using a laser confocal microscope and a scanning electron microscope. The presence of silicon inclusions in the epidermal walls of cells of the convex area (above midrids), and in cells of the stomata zone (stomata, cells surrounding the stomata, and in normal epidermal cells) on the upper and lower surfaces of cattails grown in water and in terrestrial soil was detected by laser confocal microscopy. The intensity of silicon fluorescence in the cells of the adaxial epidermis was significantly higher compared to that of the abaxial epidermis. The highest silicon content was found in epidermal cells of the convex zone, above the vascular bundles, with its content in the upper epidermis being 1.3 times higher than in the same cells of the lower epidermis. It was found that the content of silicon in the epidermis of terrestrial plants was more than that in the leaves of *T. angustifolia* grown in water. For the first time, a significant increase in the silicon content in the leaves of terrestrial plants of this species was also detected by electron microscopy and X-ray analysis. It has been established that the cells of the adaxial epidermis, particularly those above the conducting bundles (in the convex zone) and the stomata, are the main silicon accumulators. It is assumed that such localization and increased silicon content optimize the water balance of terrestrial plants and thus increase their tolerance to soil drought. It is proposed to increase attention to the study of silicon's role in plant adaptation to adverse changes in abiotic environmental conditions.

Keywords: *Typha angustifolia*, leaf, epidermis, silicon inclusions, soil drought

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Introduction

Fluctuations in soil water balance within biotopes, particularly flooding or soil drought, induce changes in the structural and functional organization of plants, thereby activating adaptive mechanisms in response to the stressor (Vartapetian & Jackson, 1997;

De Micco & Aronne, 2012; Kordyum & Dubyna, 2019). Silicon is present in plants in the form of monosilicic acid or in an amorphous or crystalline form. It has been established that silicon ions are in some way linked to plant resistance to changes in water balance; in particular, silicon enhances the lignification and suberisation of roots, accompanied by the activation of genes associated with enzymes involved in the biosynthesis of osmoprotectants, lignin and suberin (Perry & Lu, 1992; Epstein, 1999, 2009; Fleck et al., 2011; Khan, 2025). Silicon is also involved in increasing the contents of chlorophylls and carotenoids in above-ground organs and in thickening leaf cell walls (Song et al., 2014). In addition, silicon plays a role in optimizing the water balance of cells, accumulating in the cells of the leaf and stem epidermis to form a double-thickened cuticular-silicon wall, which protects the plant from excessive water loss by reducing cuticular transpiration (Kerstein, 2006; Schönherr, 2006). Within plant cells, silicon can form hydrophilic silicate-galactose complexes that bind free water, thereby increasing the water-holding capacity of the cells and the plant as a whole. Due to their denser cell walls and ability to retain moisture, silicon compounds, when present in sufficient quantities, can significantly increase plants' resistance to drought and also protect them from lodging (Hodson et al., 2005).

Given that water is one of the main factors ensuring plant growth, development and productivity, and that the leaf epidermis is the primary tissue of the above-ground organs regulating the plant's water balance (Kerstein, 2006), we set out to investigate the localisation and content of silicon ions in the leaves of aquatic and terrestrial plants of *Typha angustifolia* L. (Typhaceae), which, under natural conditions, has adapted to growing in contrasting environmental conditions, namely in water and on land. In our opinion, this species serves as a suitable natural model for studying the adaptive capacity of plants to both natural flooding and terrestrial growth. *Typha angustifolia* is a closely related monoecious aquatic-palustrine plant native to Europe, widespread in the temperate zone of the Northern Hemisphere. It is a heliophytic, light-loving, herbaceous, perennial aquatic plant, 0.8–1.5 m tall. Given that water is one of the main factors ensuring plant growth, development, and productivity, and that the leaf epidermis is the primary tissue of the above-ground organs regulating the plant's water balance, we set out to investigate the localization and content of silicon ions in the leaves of aquatic and terrestrial *T. angustifolia* plants.

Material and methods

The study involved the leaves of *T. angustifolia* plants that grew in water at depths of up to 50 cm on the left bank of the Dnieper River (in Kyiv), and on the leaves of terrestrial plants that grew on sandy soil 3–4 m from the riverbank. The material was collected in early June during the vegetative growth phase. The selected cattail leaves were fixed directly on the riverbank for cytological studies. The material was fixed in a mixture of glutaraldehyde and paraformaldehyde solutions (1:1, v/v) in phosphate buffer, pH 7.2. The fixed samples were delivered to the laboratory for analysis. The water temperature on the day of sample collection was +16 °C, and the air temperature was +21 °C. Standard biochemical methods were used to determine the relative water content in the soil and leaves.

Laser confocal microscopy

For cytochemical studies of silicon localization and content, cross sections were taken from the middle part of mature leaves. For the cytochemical analysis of silicon, these samples were processed according to the protocol of Dabney et al. (2016) and examined using a Zeiss LSM-5 laser-scanning confocal microscope at an excitation wavelength of 480 nm and an emission wavelength range of 500–530 nm. The intensity of silicon fluorescence was determined using the Pascal software. The intensity of silicon fluorescence was measured in 15–20 cells of the upper and 15–20 cells of the lower epidermis from each sample.

X-ray diffraction analysis of chemical elements

X-ray diffraction analysis of chemical elements in the leaf epidermis of two ecotypes of *T. angustifolia* was carried out following the method described by Bücking & Heyser

(2000), using a JSM-6060 LA scanning electron microscope (SEM) with a JEOL EX-S4175GMU X-ray diffraction unit and the ZAF software. For standard quantitative elemental analysis, the silicon content was determined as a percentage of the scanned mass of the leaf blades (mass%). The analysis time was 120 s at a voltage of 15 KV. The presence of the following elements was determined: Si, K, Na, Ca, Mg, Al, S, P, and Cl. The mean and standard error were determined using Student's t-test ($P < 0.05$).

Soil moisture content was determined using the standard thermostatic-gravimetric method. To determine the moisture content of the soil on which cattail plants grew, soil samples were taken at a depth of approximately 15–20 cm from the surface of dry land, and up to 10 cm from the surface of flooded soil for aquatic cattail plants. Soil samples were dried in a thermostatic oven at 105 °C to a constant weight, and moisture content was calculated from the difference. The water content in plant samples was determined using the standard gravimetric method. This involved weighing the fresh plant material and subsequently drying it in an oven at +85 °C until a constant weight was reached. It was found that the soil moisture content of the soil in which aquatic cattail plants grew was 82 ± 2.5%, whilst the soil moisture content of the soil in which terrestrial cattail plants grew was 55.3 ± 1.7%. The water content in the leaves of aquatic cattail was 65.3 ± 0.5%, and in terrestrial cattail it was 43.2 ± 0.7%.

Results

The presence and content of silicon in the leaves of narrow-leaved cattail, *T. angustifolia*, were determined on the surface of the leaf blades, the structure of which is characterized by certain features. According to SEM data we obtained previously (Nedukha, 2025), the leaves of the narrow-leaved cattail are amphistomatic (stomata on both leaf surfaces). The adaxial and abaxial surfaces were characterized by the presence of two structural zones, regardless of the growth conditions of this species: a convex vault zone (above the midribs and vessels), consisting solely of one type of ordinary epidermal cells, and a stomatal zone, in which stomata and ordinary epidermal cells were located. Two structural zones were arranged parallel to the long axis of the leaf and alternated in a specific order (Fig. 1 A–C). It should be noted that the structure of the epidermal cells was not smooth, but covered with cuticular-wax-like structures that rose above the surface by 1-3 μm.

Data from laser confocal microscopy

Leaves of Typha angustifolia plants, which grew in the water

A study of silicon in the leaves of cattail grown in water, using confocal microscopy, revealed the presence of fine (<10 nm) amorphous silicon inclusions, as well as small crystalline inclusions in the cell walls of both leaf surfaces. Silicon was present in the convex zone and all cell types in the stomatal zone, specifically in the epidermis of the guard cells of the stomata, in the epidermis of the cells surrounding the stomata, and in the main (ordinary) cells of the epidermis in this zone (Fig. 1 D, E). Amorphous silicon inclusions covered the epidermis in a continuous layer (green fluorescence), as evidenced by 3D reconstructions from 12 consecutive sections through the sample. However, on standard sections (thickness of 1.2–1.5 μm), the silicon structures varied in shape – from rounded, teardrop-shaped, and rod-shaped to square, with dimensions exceeding 10 μm (Fig. 1 F, G). These silicon structures can be classified as crystalline inclusions. The use of the Pascal program enabled the determination of the relative content of silicon inclusions in the investigated samples.

It was found that the relative fluorescence intensity of amorphous and crystalline silicon inclusions depended on the structural zone of the epidermis, the cell type, and the leaf surface (Table 1; Fig. 1 F′, G′). The intensity of silicon fluorescence in the cells of the adaxial epidermis was significantly higher compared to that of the abaxial epidermis. The highest silicon content was found in epidermal cells of the protuberance/convex zone, above the vascular bundles, with the upper epidermis containing 1.3 times as much as the same cells in the lower epidermis. In the lower epidermis, the guard cells of the stomata and ordinary cells also contained less silicon than the cells of the convex zone. In terms of silicon content,

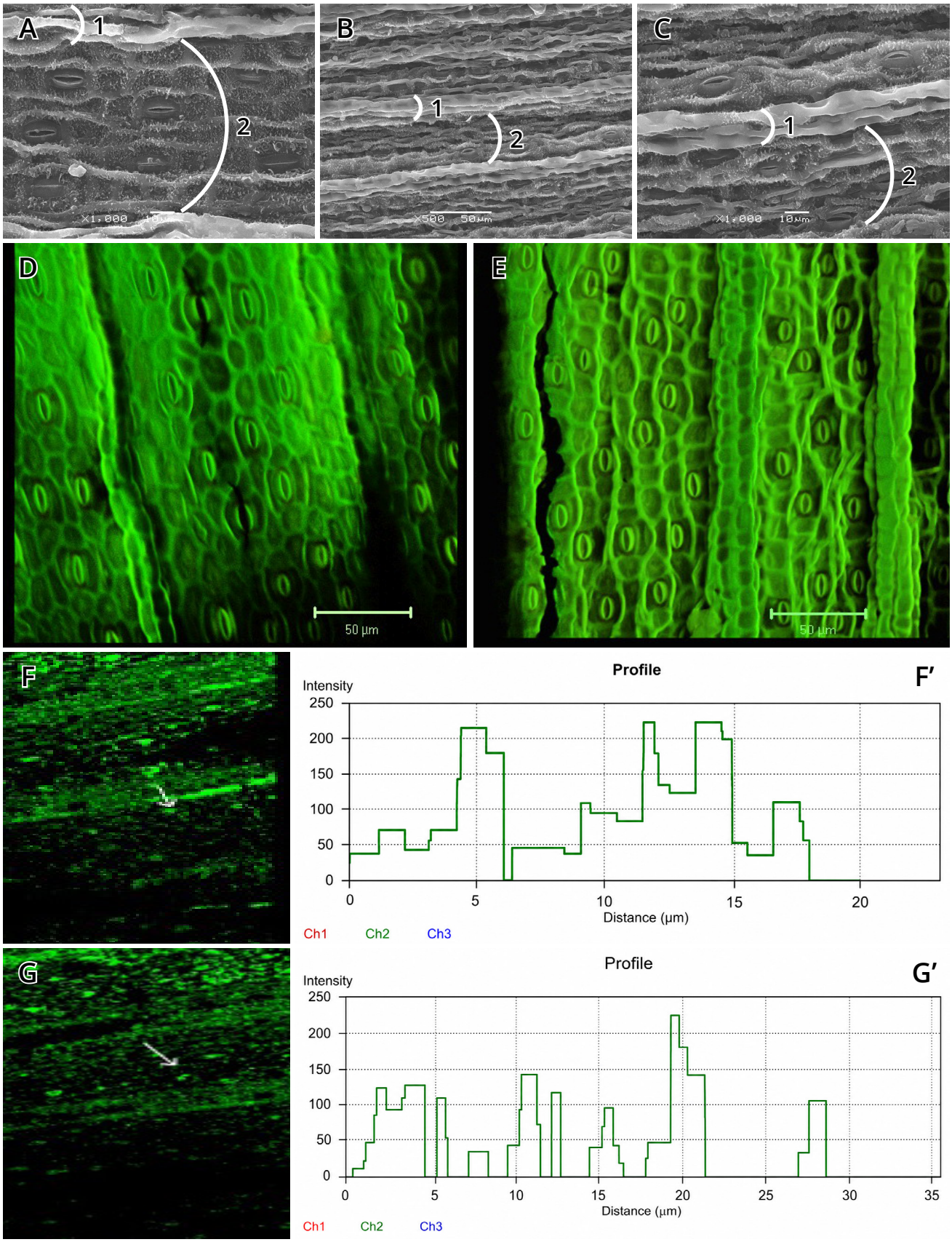

Figure 1. SEM micrographs of leaves in *Typha angustifolia* plants grown in water (**A, B** – adaxial surface) and in terrestrial soil (**C** – adaxial surface): **1** – convex zone; **2** – stomata zone. Confocal microscopy of silicon fluorescence (green color) on adaxial (**D, F**) and abaxial (**E, G**) surfaces of leaves in water plants of *T. angustifolia*. **D, E** – 3D photographic images of adaxial and abaxial surfaces received by stacking of 12 serial scanning micrographs. **F′, G′** – histograms of fluorescence intensity of silicon (green line) in the distances indicated on figures F and G, respectively.

Table 1. Fluorescence intensity of silicon in the leaf epidermal cells of *Typha angustifolia* plants, which grew in natural conditions: in water and on terrestrial soil. The data were obtained using a Pascal program during analysis on a laser confocal microscope.

Ecotype	Leaf surface	Fluorescence intensity of Si, relative units			
		Convex zone (above the midrids and vessels)	Stomata zone		
			Stomata guard cells	Cells surrounding the stomata	Usual epidermal cells
Air-water plants	Adaxial	154 ± 13.9	135 ± 12.9	81 ± 4.9	97 ± 7.2
	Abaxial	125 ± 11.1	89 ± 5.7	77 ± 5.8	65 ± 4.9
Terrestrial plants	Adaxial	201 ± 17.5	165 ± 14.1	110 ± 9.8	131 ± 12.1
	Abaxial	164 ± 13.1	136 ± 11.4	123 ± 11.2	85 ± 6.7

the cells can be ranked as follows: ridge zone > stomata > cells surrounding the stomata > ordinary epidermal cells.

Leaves of Typha angustifolia plants, which grew in terrestrial soil

Study of silicon in the leaves of cattail growing on dry land shown that with using laser confocal microscopy, the presence of fine (<10 nm) amorphous silicon inclusions, as well as small crystalline inclusions in the epidermis cells of two structural zones (Fig. 2 A, B) on both the upper and lower surfaces of the cattail leaf blades, namely: in the cells of the convex zone, as well as in all cells of the stomatal zone. Amorphous silicon inclusions covered the epidermis in a continuous layer, just as in the leaves of *T. angustifolia* grown in water.

It was found that the relative fluorescence intensity of amorphous and crystalline silicon inclusions in terrestrial plants also depended on the structural zone of the leaf epidermis, the cell type, and the leaf surface (Table 2; Fig. 2 C, D, C', D'). The highest silicon content was found in the epidermal cells of the convex zone in comparison with that in the corresponding cells of the lower epidermis. In the lower epidermis, guard cells and ordinary cells also contained less silicon than the cells of the convex zone. In terms of silicon content, the cells can be ranked as follows: convex zone cells > stomata > cells surrounding the stomata > ordinary epidermal cells. That is, this order is similar to that in the leaves of plants growing in water. The presence of silicon in the cells of the adaxial and abaxial epidermis of the studied ecotypes of narrow-leaved cattail, regardless of the site of growth, was also established using X-ray diffraction analysis (Fig. 3).

X-ray structural analysis of leaves

Leaves of Typha angustifolia plants, which grew in the water

Scattering X-ray structural analysis of chemical elements in cells from two structural zones – the papillae zone and the stomata zone – revealed the presence of silicon on both sides of the cattail leaf blades, regardless of the type of epidermal cells (Fig. 3 A, B). The silicon content in the cells of the adaxial surface was low, at 0.09% in the convex zone (above the veins) and 0.07–0.08% in guard and ordinary epidermal cells. In the cells of the abaxial surface of the epidermis, silicon content was lower: 0.05% in the convex zone and 0.01–0.02% in the stomata and surrounding ordinary epidermal cells. In addition to silicon, other elements were detected in the leaf cells, including K, Na, Ca, Mg, Al, S, P, Si, and Cl.

Leaves of Typha angustifolia plants, which grew in terrestrial soil

X-ray analysis using an electron microscope also showed that the silicon content in the leaves of the terrestrial plants of *T. angustifolia* was higher compared to that in the cattail growing in water (Fig. 3 C). On the upper surface, in the cells of the papillary zone, it was 0.09%. In the stomata zone it was: in the guard cells of the stomata – 0.15%; in the cells surrounding the stomata and in the

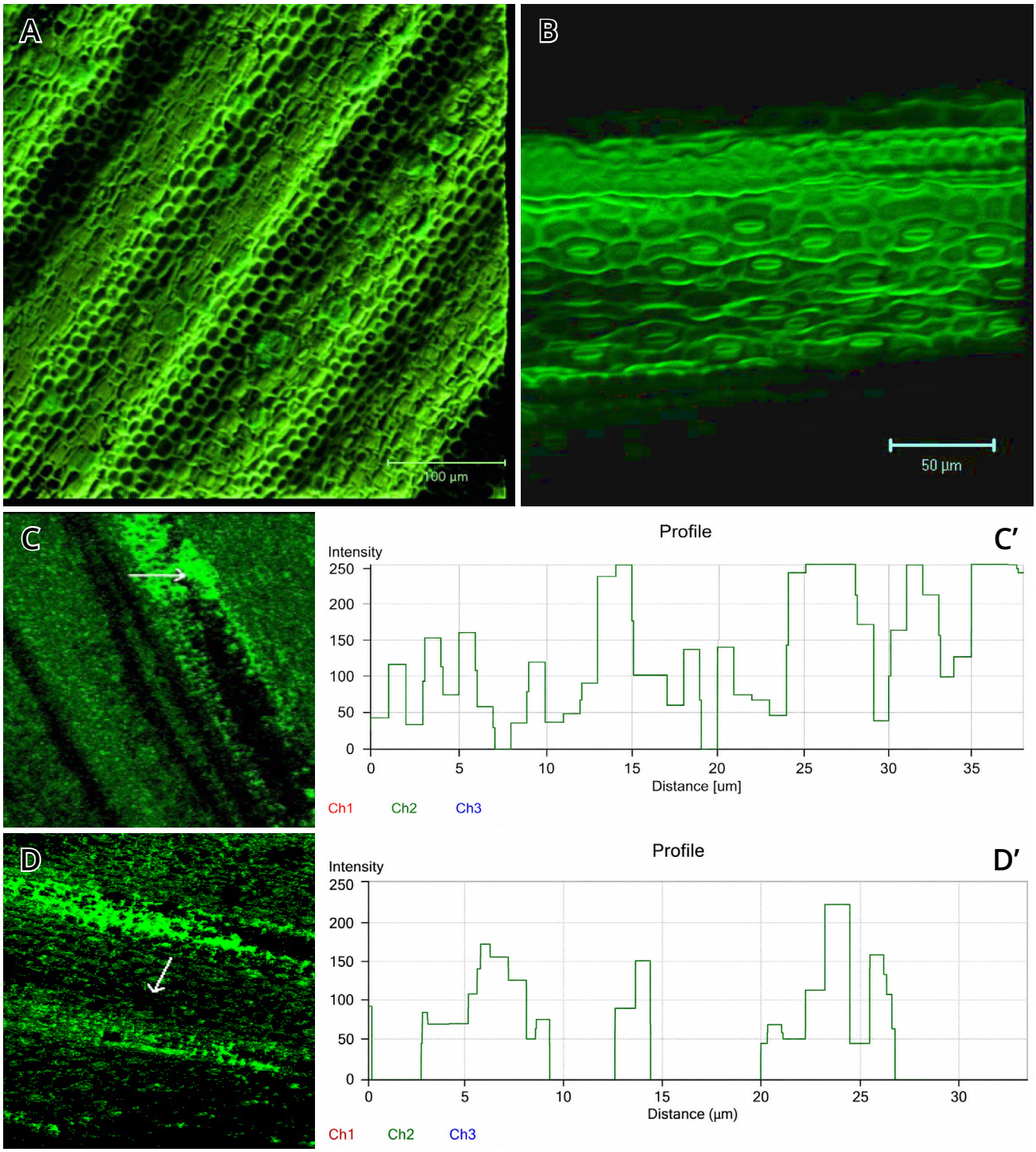

Figure 2. Confocal microscopy of silicon fluorescence (green color) on adaxial (**A, C**) and abaxial (**B, D**) surfaces of the leaves in *Typha angustifolia* plants, grown in terrestrial soil. **A, B** – 3D photographic images of adaxial and abaxial surfaces received by stacking of 12 serial scanning micrographs. **C′, D′** – histograms of fluorescence intensity of silicon (green line) in the distances indicated on figures F and G, respectively.

ordinary epidermal cells – 0.46% and 0.68%, respectively. On the lower surface of the leaf, the silicon content was lower than on the upper surface and amounted to the following: in the convex zone – 0.07%, in the stomata – 0.10%, in the cells surrounding the stomata – 0.27%, and in ordinary epidermal cells – 0.46%, respectively. The other elements were also detected in the leaf cells, including K, Na, Ca, Mg, Al, S, P, Si, and Cl.

Table 2. Silicon content in the leaf epidermal cells of *Typha angustifolia* plants, which grew in natural conditions: in water and on terrestrial soil. The data were determined by X-ray diffraction analysis using a scanning electron microscope.

Ecotype	Leaf surface	Si content, %mass			
		Convex zone (above the midrids and vessels)	Stomata zone		
			Stomata guard cells	Cells surrounding the stomata	Usual epidermal cells
Air-water plants	Adaxial	0.09 ± 0.01	0.08 ± 0.01	0.08 ± 0.002	0.07 ± 0.005
	Abaxial	0.05 ± 0.009	0.01± 0.001	0.01 ± 0.001	0.02 ± 0.001
Terrestrial plants	Adaxial	0.09 ± 0.001	0.15 ± 0.001	0.46 ± 0.002	0.68 ± 0.004
	Abaxial	0.07 ± 0.001	0.10 ± 0.001	0.27 ± 0.001	0.43 ± 0.001

Discussion

Previous comparative studies of the leaves of aquatic and terrestrial plants of *T. angustifolia* have shown similarities in leaf morphology (Nedukha, 2025). Our findings on the silicon content in cattail leaves showed that, regardless of the plant's growing conditions, silicon is present in all types of epidermal cells: above the veins (in the convex zone) and in the stomata and cells surrounding the stomata (in the stomatal zone). The form of silicon we detected in the leaves of common reed was predominantly amorphous, and only occasionally did we observe crystal-like structures when examining individual (1–1.5 μm thick) sections. A similar silicon structure has also been previously described in the leaves of *Phragmites australis* (Cav.). Trin. ex Steud. (Poaceae) growing in water and on land (Nedukha, 2018). However, the silicon content was higher in the leaves of terrestrial plants. To explain this phenomenon, it should also be noted that the relative water content in the leaves of aquatic plants was 65.3 ± 0.5% at a soil moisture content of 82.0 ± 2.5%, and in terrestrial plants, it was 65.3 ± 0.5% and a soil moisture content of 43.2 ± 0.7%.

We hypothesize that increased silicon content in the leaf epidermis of these plants plays a significant role in maintaining optimal cellular water balance in terrestrial plants. Silicon is known to be absorbed by the root system and deposited in the cell walls of leaves and stems (Ma & Takahashi, 2002; Raven, 2003), thereby thickening the cell wall and enhancing suberinisation and lignification of cells (Suzuki et al., 2012). The thickened cuticular-silica wall in all types of *T. angustifolia* epidermal cells protects the plant from excessive water loss, reduces cuticular transpiration, and increases resistance to lodging and to drought and oxidative stress compared to aquatic plants of this species grown in water (under high soil moisture conditions).

We detected silicon ions in the stomata of leaves, regardless of the ecotype of *T. angustifolia*. It is known that water evaporation promotes the condensation of salts in the xylem and contributes to the formation of soluble deposits, including silica. Although most of the water evaporates from the epidermal and mesophyll cells and passes through the stomata into the atmosphere, silicon deposition in the cells occurs gradually. It increases with plant age (Motomura et al., 2008), especially over the cells of the midribs and conducting bundles, which provide crucial structural-mechanical support to keep the leaf flat and upright for sunlight exposure and act as a vascular highway to transport water, minerals, and aqueous solutions of sugars between the stem and leaves (Coomes et al., 2008; Taneda & Terashima, 2012). Perhaps this is why the stomatal guard cells in *T. angustifolia* leaves exhibit weaker silicon fluorescence than epidermal cells above the veins and vessels (in the convex zone).

It is known that silicon reduces water evaporation from the leaf surface, even in the absence of stress, as demonstrated in rice seedlings (Ma & Takahashi, 1993), on drought-tolerant wheat seedlings (Gong et al., 2005),

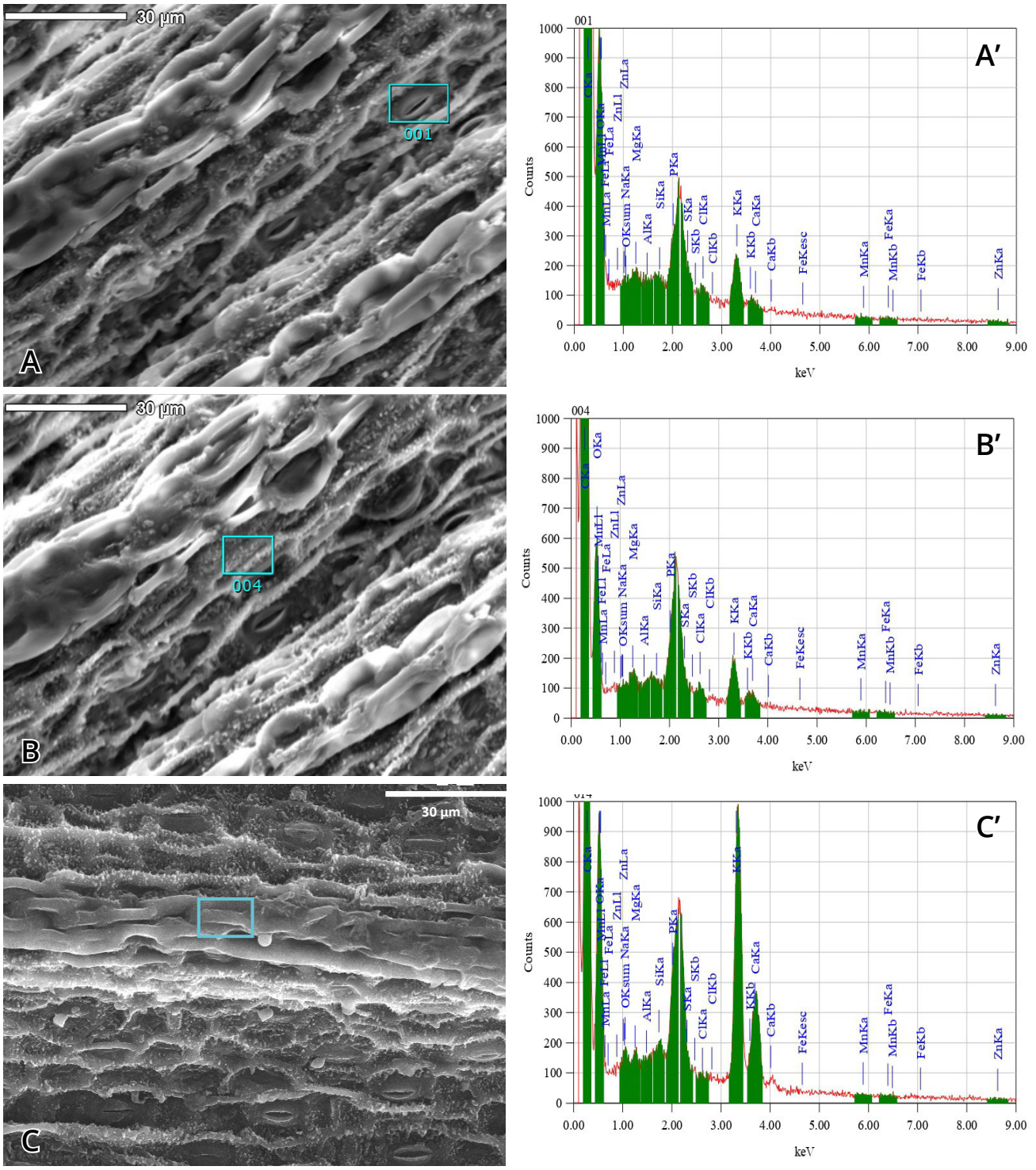

Figure 3. Micrographs of different epidermal cells with spectra of Si and other ions measured by the X-ray technique of *Typha angustifolia* air-aquatic (A, B) and terrestrial (C) plants at the vegetative stage of growth. On the left side of each figure (**A, B, C**), outlined in the green square is the cell or part of the epidermis surface that was investigated by the X-ray method. On the right side of each figure (**A', B', C'**) is the histogram of the content of chemical elements, including silicon. The axes on C′ and D′: y-axis shows counts per second (cps), notably impulses eV per second; and x-axis shows energy in keV (kilo-electron volts).

and sorghum (Hattori et al., 2005; Ahmed et al., 2011). It is also worth noting another function of silicon – namely, its influence on water transport and the regulation of cell osmotic potential (Pei et al., 2010; Ming et al., 2012).

In cell walls, silicon forms part of hydrophilic silicate-galactose complexes, including pectin and callose, which bind free water, thereby enhancing the water-holding capacity of cells and significantly

increasing plant drought tolerance whilst providing mechanical support to plants (Guerriero et al., 2016). Taking into account these data and the findings regarding increased silicon content in the terrestrial cattail, it can be assumed that the aquatic and terrestrial ecotypes of *T. angustifolia* differ significantly in terms of both water uptake and water consumption, as well as in the different speed of silicon synthesis and accumulation. The mechanisms underlying these processes require further study.

It has previously been established that silicon can also activate water transport from the root system to the leaves by regulating the function of aquaporins (water channel proteins in the cytoplasmic membrane and organelle membranes) and by influencing the osmotic potential of cells (Hodson et al., 2005; Pei et al., 2010; Ming et al., 2012). Furthermore, the increase in silicon content in the leaves of the terrestrial *T. angustifolia* plants may be mediated by the activation of numerous genes encoding various proteins, including transcription factors associated with the ethylene-sensitive stress signaling pathway, which ensure the stability of proteins and nucleic acids by preventing their denaturation during dehydration (Rotat, 2006).

The effect of silicon on the expression of genes encoding dehydratases during dehydration of *Oryza sativa* L. (Poaceae) plants under drought and osmotic stress has been established (Liu et al., 2014). Based on an analysis of literature data and our own findings, it can be suggested that it is precisely the increased accumulation of silicon in the epidermal cells of terrestrial plants that helps maintain optimal water status of plants when soil moisture decreases and is one of the factors determining the widespread distribution of *T. angustifolia* in ecologically diverse regions of Ukraine and Europe. Thus, the data obtained indicate the potential for further research into the role of silicon in plant adaptation to adverse environmental changes in natural communities and agrocoenoses, given the current increase in anthropogenic pressure and projected global climate change.

Conclusions

The research was conducted using comprehensive modern and classical approaches. The results are fundamental and contribute to our understanding of the mechanisms underlying phenotypic plasticity in plants growing under various natural conditions, which is important for the conservation of aquatic vegetation.

Using cytochemical methods involving laser confocal microscopy and X-ray analysis, the presence of silica ions in the epidermis of the leaves of aquatic and terrestrial cattail plants (*Typha angustifolia*) was established, and their content depended on the ecotype and the surface of the leaf epidermis. For the first time, a significant increase in the silicon content in the leaves of terrestrial plants of this species was detected by electron microscopy with X-ray analysis. It was established that the cells of the adaxial epidermis, particularly those above the conductive bundles (in the convex zone) and the stomata, are the main silicon accumulators.

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Роль іонів кремнію в стійкості рослин *Typha angustifolia* до зниження вологості в ґрунті

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Представлено результати дослідження локалізації та вмісту кремнію в листках рослин рогозу вузьколистого (*Typha angustifolia*), які зростали в природних умовах на березі Венеціанської затоки (в зоні Києва): у воді та на суходолі. Для визначення локалізації та вмісту кремнію в листках використовували цитохімічні та ультраструктурні методи. Для дослідження брали листки у фазі вегетативного росту. Наявність та локалізацію іонів кремнію вивчали із використанням лазерної конфокальної та сканувальної електронної мікроскопії. Методом лазерної конфокальної мікроскопії встановлено наявність кремнієвих включень у стінках епідермісу клітин над жилками, у продихах, клітинах, що оточували продихи, та у звичайних епідермальних клітинах на верхній та нижній поверхнях рогозу, що зростав у воді та на суходолі. Інтенсивність флуоресценції кремнію в клітинах адаксіального епідермісу була значно вищою порівняно з абаксіальним епідермісом. Найвищий вміст кремнію виявлено в епідермальних клітинах зони пагорбів (над судинними пучками), причому його вміст у верхньому шарі епідермісу був у 1,3 раза вищим, ніж у тих самих клітинах нижнього епідермісу. Також було виявлено, що епідерміс усіх досліджених типів клітин у суходільних рослин містив більше кремнію, ніж клітини рогозу, що ріс у воді. Нами також було встановлено значне підвищення вмісту кремнію у листках суходільних рослин цього виду методами електронної мікроскопії та рентгенівського аналізу. Встановлено, що клітини адаксіального епідермісу, зокрема клітини у зоні пагорбів та продихів, є головними акумуляторами кремнію. Припускається, що така локалізація та підвищений вміст кремнію оптимізують водний баланс суходільних рослин і таким чином сприяють підвищенню їхньої стійкості до ґрунтової посухи. Пропонується посилити увагу до вивчення ролі кремнію в адаптації рослин до несприятливих змін абіотичних факторів довкілля.

Ключові слова: *Typha angustifolia*, листок, епідерміс, кремнієві включення, ґрунтова посуха