

The role of silicon in plant under normal conditions and stress

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Abstract

The paper is a review view data on the role of silicon (Si) in the physiology of higher taxa plants; data on the synthesis and localization of Si in cells, as well as its participation in the mechanisms of tolerance and plasticity of plants under the influence of adverse environmental conditions. The unique physical properties of silicon are described, which explain its bioactivity as a regulator of absorption and reflection of sunlight, as well as a regulator of photosynthesis. The role of silicon in the regulation of water balance and transpiration of plants, in the protection of plant cells for the action of biotic and abiotic stresses by including protective mechanisms at the level of the organs, tissue and cell are shown. Recent studies have shown some homology of aquaporin proteins and silicon transporters. Particular attention is paid to the effect of silicon on the expression of genes involved in the synthesis of osmotic substances and secondary metabolites with protective properties. The study confirms that the conceptual basis for the protection and preservation of flora from abiotic and biotic stresses may be the preservation and reproduction of species characterized by increased silicon uptake and accumulation of this ion in plant organs. Thus, the obtained data indicate the prospects of further studies of silicon participation in plant adaptation to adverse changes upon environmental factors in natural ecosystems or agrocoenosis with modern conditions of increasing anthropogenic pressure and forecast of global climate change.

Keywords: abiotic and biotic stress; cell wall; genes; plant tolerance; silicon

Introduction

Early studies of silicon (Si) have shown that Si is one of the most widely prevailing chemical elements of Earth, which plants use in mineral nutrition and within cell structure. The content of Si is 28.8% of dry matter, and varies from 50 to 400 grams per kilogram of soil. In nature, silica can be found in solid, liquid or absorptive state, in particular in silicon dioxide (SiO_2), silica ($\text{SiO}_2 \cdot n\text{H}_2\text{O}$), and oligo- and poly silicon acids (H_2SiO_3 , H_4SiO_4). Si is part of clay minerals and silicates, while pure silicon is found as quartz, opal and other structures (Kovda, 1973; Matychenkov, 2008). Most of the reviews are devoted to the role of silicon in the life of freshwater and marine macro- and microalgae, including the formation of complex skeletal structures, such as the diatom frustule, intricate skeletons and scales covering chrysophytes. The formation of skeletal structures in alga requires a metabolic investment in silicic acid acquisition and the establishment of the silicic acid gradient between the external environment and the inner structure of cells. This data is used by researchers for

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the evolutionary history of alga silicification and for systematic and phylogenetic studies (Fu *et al.*, 2000; Hirota *et al.*, 2010; Ichinomiya *et al.*, 2011; Finkel, 2016).

An analysis of the literature on the study of silicification of higher plants, including numerous species of natural flora and species of agricultural plants, showed that a lot of work has been devoted to this issue. The reviews and/or extended experimental studies dealt with narrow issues of plant silicification. A certain part of the research was devoted to general questions about the forms of silicon that are found in tissues of higher plants (Epstein, 2009; Sauer *et al.*, 2009; Nedukha and Kordyum, 2019; Tripathi *et al.*, 2021), absorption of silicon from the soil (Knight and Kinrade, 2001; Sauer *et al.*, 2006; 2009; Mitani *et al.*, 2008; More *et al.*, 2019), silicon transport through tissues (Ma *et al.*, 2006; Ma and Yamaji, 2015; Tripathi *et al.*, 2021), silicon localization in tissues and cells (Neumann *et al.*, 1997; Neumann, 2003; He *et al.*, 2015; Manivannan and Ahn Yul-Kuyn, 2017), the protective functions of silicon during abiotic and biotic stress (Ma *et al.*, 2008; Bockhaven *et al.*, 2013; Khattab *et al.*, 2014; Manivannan and Ahn Yul-Kuyn, 2017), as well as the molecular mechanisms in which silicon (Song *et al.*, 2014) is involved. In the hereby review, authors tried to combine the available data in order to synthesize recent advances of the biochemical and functional properties of silicon in the plant cell and identifies areas for further study. A new specific feature of the interaction of silicon with the functional load of a particular cell and tissue under certain conditions of plant growth was described. It can also facilitate the development of chemical additives (to fertilizers) to increase the resistance of cultivated and wild species to global warming on Earth. The review is necessary for researchers in the field of botany, plant physiology, phytopathology, agriculture, and ecology, for whom testing of the resistance and adaptation of plants to drought, changes in soil water balance or protection of the root system from toxic ions in the soil can be carried out using a simple marker the presence of silicon inclusions in the leaf epidermis or in the formation of nano-silicon film around the roots (Feng *et al.*, 2019).

The study of silicification of different species of wild and cultivated plants shown that silicon can be found in plants under three forms: soluble (in the form of acid), associated with high-molecular organic compounds, in pure amorphous (silicon dioxide) and/or crystalline form (Epstein, 1999; Kolesnikov, 2001, Neumann, 2003). Amorphous silica consists of ultimate particles of the inorganic polymer (SiO_2), where a silicon atom is covalently bonded in a tetrahedral arrangement to four oxygen atoms (Figure 1A). Each of the four oxygen atoms is covalently bonded to at least one silicon atom to form either a siloxane, $-\text{Si}-\text{O}-\text{Si}-$, or a silanol, $-\text{Si}-\text{O}-\text{H}-$, functionality. In the majority of crystal inclusions, silicon atom shows tetrahedral coordination with four oxygen atoms surrounding a central Si atom. The most common example is seen in the quartz polymorphous. It is a 3-dimensional network solid in which each silicon atom is covalently bonded in a tetrahedral manner to 4 oxygen atoms (Figure 1B). Silicon ions in higher plants can bind to proteins, amino acids, polysaccharides, phenols, lipids and other substances; when bound to amino acids and carboxylic acids, silicon forms orthosilicon esters. In cell walls, silicon binds to hydroxide groups of polysaccharides, forming a Si-O-C bonds; in cytoplasm it binds to oxygen of amino acids of proteins, forming Si-O bonds, and also to amino acid groups Si-NH bonds (Figure 1C) (Kolesnikov, 2001).

In soil, silicon has the function of an activator for the transformation of hard-soluble to readily soluble micro elements which are necessary for plants (Farmer *et al.*, 2005). The study of physical-chemical characteristics of silicon in plants showed that the functions of silicon in plant cells are associated with plants' metabolism. Deposited in the epidermis of the vegetative organs, silicon can reflect part of the light, or absorb (Ma *et al.*, 2011), and thus regulates the intensity of photosynthesis (Watanabe *et al.*, 2004; Song *et al.*, 2014). Silicon deposits in the leaf epidermis also delay transpiration (Gong *et al.*, 2005; Hattori *et al.*, 2008; Ahmed *et al.*, 2011), which optimizes the water balance of cells and organs and thus the whole plant (Nedukha and Kordyum, 2019). Later, silicon was recognized as a chemical element involved in the adaptation of plants to adverse abiotic factors: drought (Takasaki *et al.*, 2010; Song *et al.*, 2011; Khattab *et al.*, 2014), soil salinity (Liang *et al.*, 2006; Shi *et al.*, 2016), soil contamination with toxic metals and semi-metals (Liang *et al.*, 2005; da Cunha *et al.*, 2008; Naeem *et al.*, 2014; Feng *et al.*, 2019; More *et al.*, 2019). The involvement of silicon in plants' resistance to pathogen invasion has also been established (Perry and Keeling-Tuckern, 2003; Rodrigues

et al., 2003). Using gene sequencing techniques, it has been clearly shown that silicon is involved in the expression of genes *Os03g57120* and *Os09g26810*, *PsbY* (*Os08g02630*), which encode chloroplast proteins responsible for electron transport in photosynthesis (Breyton *et al.*, 1994; Kawakami *et al.*, 2007) and encode proteins of cell wall that prevent pathogen invasion (Fauteux *et al.*, 2005).

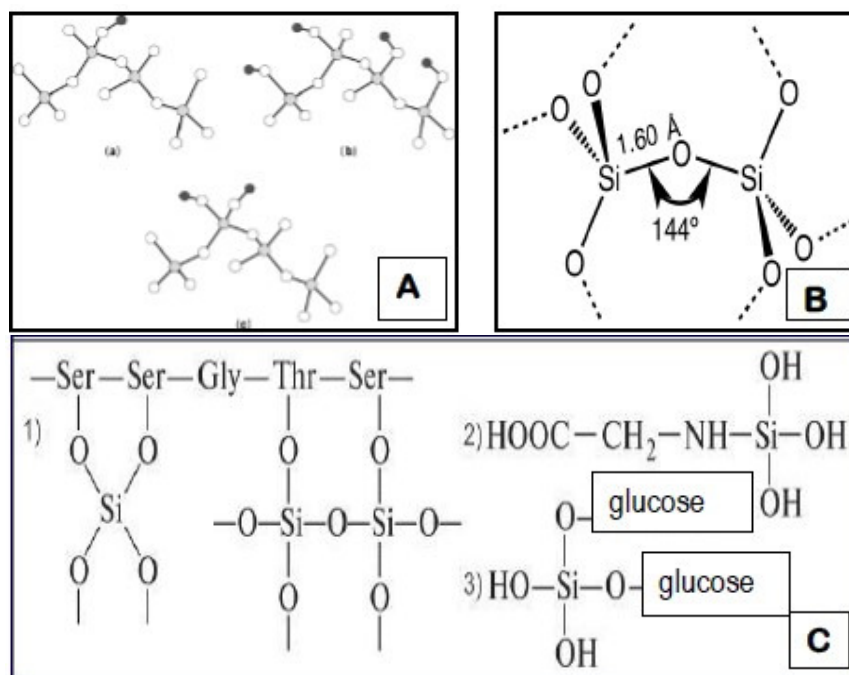


Figure 1. Structural motif found in amorphous silica (A), where (a) isolated, (b) vicinal, and (c) germinal type; (B) α -quartz (crystalline domains) of silicon dioxide is presented. (C) - Shapes of silicon bonds with organic substances are presented, where 1) Si bond with amino acid oxy groups of amino acids; 2) Si bond with nitrogen molecules of amino acids; 3) Si bond with oxygen and carbon of hydroxyl groups of sugar residues. (Kolesnikov, 2001)

Absorption and synthesis of silicon in plants

All plants, by their ability to absorb silicon from their roots, are divided into three types: strongly accumulating, accumulating and weak accumulating silicon. Silicon is useful for plants for growing under both normal and stress conditions (Epstein, 1999, 2009; Knight and Kinrade, 2001). Silicon in the soil has the function of an activator for the transformation of hard-soluble to readily soluble microelements (Farmer *et al.*, 2005; Rezanka and Sigler, 2008). Since the discovery of silicon transporters, more than 500 plants species have been investigated to elucidate the mechanisms of silicon uptake and transport. The experimental species were different in high or little silicon content. Among them, monocotyledons, such as rice, wheat, corn and barley, are classified as natural Si accumulators with 10-15% (Hodson *et al.*, 2005; Ma *et al.*, 2006).

Absorption of silicic acid

Silicon is absorbed by plant roots in the form of silicic acid, which has been dissolved in ground water. Silicon acid is transported to the root tissue as a monomer molecule. Silicon is transported through the root tissues in two ways: actively, in an energy-dependent process or passively, in an energy independent way, due to the electrochemical gradient. Biological membranes show basal permeability for silicon acid (coefficient permeability is $10^{-10} \text{ M} \cdot \text{s}^{-1}$ (Raven, 2001). Silicon acid moves through the lipid layer of the cytoplasmic

membrane either inside or out of the cell. Like an uncharged molecule, silicon acid is transported inside or out of the cell (Exley, 2009). Absorption of silicon can also occur through leaves when plants are sprayed with silicon-containing solutions (Matychenkov, 2008). The transport of silicic acid from soil to the root tissues and then to the stem and leaves occurs with the participation of several transporter proteins (channel-type transporters and efflux transporters). The first Si transporter (OsLsi1) was identified in rice (Ma *et al.*, 2006); this protein is a bidirectional passive channel (Mitani *et al.*, 2008; Mitani *et al.*, 2009). The channel-type transporters, which were identified in different species, were like an OsLsi1 (Ma and Yamaji, 2015). These proteins belong to the NIP subfamily, which is similar to aquaporin. Lsi1 (Low Si1) is a directional passive channel; it functions in the roots only for silicon intake into the cell. Lsi1 protein shows high similarity of sequences with aquaporin NIP-26 (nodulin-26 like an intrinsic protein) with a subfamily of plant aquaporin's (Ma *et al.*, 2007b). This protein is mainly localized in the roots on the distal side of the exoderm and the endoderm, where the silicon flow decreases at the border with the apoplast. Further, silicon from the cells of the exoderm and endoderm passes through the apoplast of aerenchyma using another type of protein Lsi2 transporter (efflux transporter, Lsi2), which works in the presence of proton gradient on the plasma membrane (Ma *et al.*, 2007a; Ma and Yamaji, 2015). That is, the transport of silicon acid inside the exoderm is carried out by the functioning of Lsi1-transporters. The exit of silicon acid from xylem and the pass into the aerenchyma occurs with the participation of another type of protein-transporter (Lsi2). Protein Lsi2 belongs to the family of anionic transporters. It works only so that active Si exits the cell, this protein is localized to plasma membrane located on the proximal side of the exodermis and the endodermis (Ma *et al.*, 2007b). Thus, for accumulation and uptake of Si in cells and/or tissues, it occurs the cooperation of Si influx and efflux transporters, which are diametrically localized in the cell. This occurs owing to specificity of the localization of both Lsi1 type Si channels and Lsi2-type Si efflux transporters. Subsequently, Si, in the form of silicon acid, is transported to shoots and leaves by xylem due to osmosis and transpiration. The transporter responsible for xylem transport of Si has not yet been identified.

Based on a study of silicic acid transporter proteins in rice, corn and barley plants, Mitani *et al.* (2008) proposed the presence of a cooperative system for transporting $\text{Si}(\text{OH})_4$ from soil to the root and then into the above ground organs. This system consists of several stages of silicon transport from soil to plant root, including its uptake, xylem unloading and distribution of Si in stem and leaves:

- 1) The influx transport of $\text{Si}(\text{OH})_4$ first occurs by the transporter Lsi1 from the soil to cells of the root epidermis, then to the cells of the cortex and the endoderm (casparian strip) root. The transport of silic acid goes in one direction from the epidermis to the endoderm;
- 2) The efflux of silicic acid occurs by Lsi2 transporter from endoderm cells to the root xylem. Lsi2 transporter is localized only on the proximal side of the cell adjacent to the xylem cells. Along the xylem silicic acid is transported together with xylem juice to leaf vessels;
- 3) The efflux transport of $\text{Si}(\text{OH})_4$ (with xylem juice) from the xylem cells of the conductive bundles of the leaf, to the first layer of parenchyma cells (mesophyll), occurs with the participation of the Lsi6 transporter; then silicic acid is directed both to the leaf epidermis cells and to other parenchyma cells of mesophyll through the apoplast and/or the symplast. But the transporters of this pathway are still unknown (Mitani *et al.*, 2008).

Synthesis of silicon inclusions in cells

Aqueous silicic acid solution comes from the xylem of the conductive bundles to the leaf mesophyll and epidermis cells, where it transforms into semi-solid amorphous or crystalline silicon in apoplast and/or intracellular space (Ma *et al.*, 2011). Silicon in plant cells can be in three forms: soluble (in the form of acid), associated with high-molecular organic compounds, or in pure amorphous or crystalline form. According to Müller and Grachev (2009) amorphous, hydrated and polymerized silicon material are presented as the next composition: $\text{SiO}_2 \cdot n\text{H}_2\text{O}$ or $\text{SiO}_{2-x}(\text{OH})_{2x} \cdot 2\text{H}_2\text{O}$. For formation of dimers and small oligomers from ortho-silicic acid, occurs by removal of water: $2\text{Si}(\text{OH})_4 \leftrightarrow (\text{HO})_3\text{Si}-\text{O}-\text{Si}(\text{OH})_3 + \text{H}_2\text{O}$. Silicon ions in plant cell

can bind to proteins, amino acids, polysaccharides, polyphenols, lipids and other substances; when bound to oxy-amino acids and oxy-carboxylic acids, silicon forms ortho-silicon esters. In cell walls, silicon binds to hydroxyl groups of polysaccharides, forming a Si-O-C bond; in cytoplasm, it binds to oxygen of the oxy-groups of proteins, forming a Si-O bond, and also to amino acid groups - Si-NH bonds (Kolesnikov, 2001; Müller and Grachev, 2009). The content and ratio in cells of these three forms of silicon depends on the organ, tissue type, growth and development phase of the plant (Fleck *et al.*, 2011; He *et al.*, 2015). It is estimated that 90% of absorbed Si precipitate in the cell walls of leaf epidermis, and this is up to 10% of the dry mass of herbaceous plants (Yoshida, 1965; Ma and Takahashi, 2002; Raven, 2003).

Silicon plays a key role in the growth and differentiation of cells of the epidermis of leaves and stems in usual conditions, as well as cell protection under biotic and abiotic stresses. In different types of epidermal and mesophyll cells, this ion is different in structure and content. But silicon is not synthesized in all cell walls; its synthesis in the plant is tissue specific, both in leaves and roots, mainly in cereals (Ma and Takahashi, 2002; Fleck *et al.*, 2011; 2015). Silicon gives mechanical strength to cell walls, which prevents the plants from being lodged (fallen). Si improves the exchange of nitrogen and phosphorus in tissues. Silicon reduces transpiration under changing the inclination of the leaves to light, or by twisting the leaf plate. Optimization of silicon consumption leads to increased leaf area, create favorable conditions for photosynthesis and stimulate root system development (Kemecheva, 2003). In addition, this element reduces the harmful effects of UV radiation (Ma and Yamaji, 2006) and increases the frost resistance of plants, particularly for wheat. One mechanism of all these effects may be the ability of silicon to induce stress proteins synthesis (Wang *et al.*, 2005).

Silicon can be in different state in cells of one tissue. This phenomenon was observed in leaves of *Týpha angustifolia* at vegetative stage. Cytochemical study of leaves was performed, using stain of Si by solution of methyl red and crystal violet lacton and revealed individual crystals of Si (Figure 2A, red arrows) and clusters of amorphous silicon with Si crystals (black arrows) that were clearly visible in the intercellular spaces near the vascular bundle and within the interspace of mesophyll (Figure 2B, yellow arrows). The presence of silicon in the cell walls of the epidermis (Figure 2C), including inside the guard cells of the stomata, can also observed as a sharp image. The silicon was also shown in the cell walls and into cells of the collenchyma, near the vascular bundle (Figure 2D, arrows).

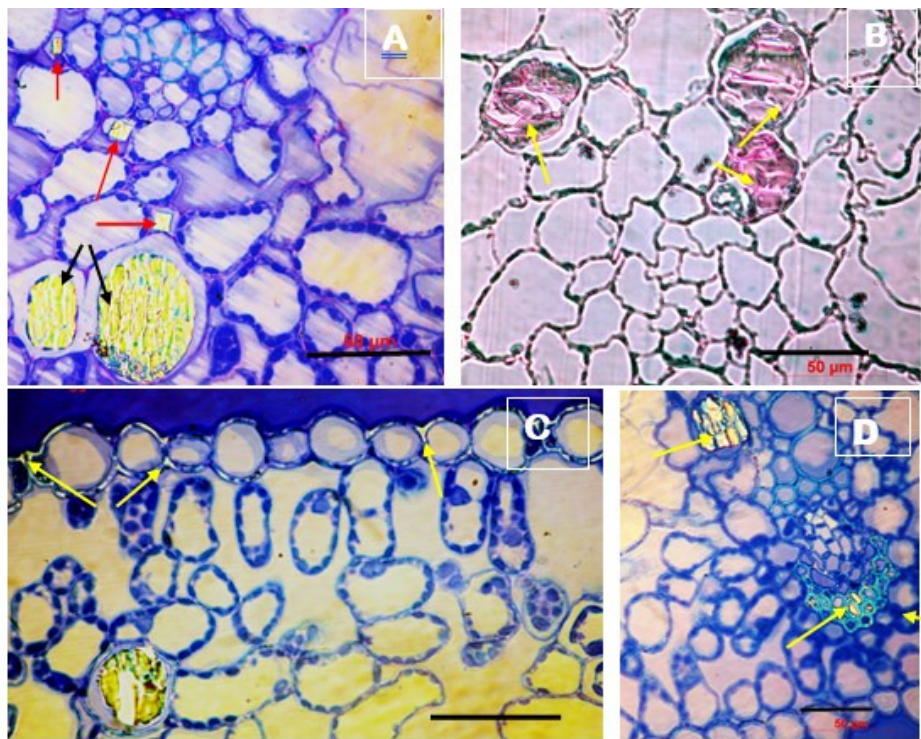


Figure 2. - Light optical microphotographs of silica in leaf of *Typha angustifolia*, grown on the sandy bank of the Dnipro River (on the outskirts of Kiev, Ukraine). Individual crystals of Si (red arrows) and clusters of amorphous silicon with Si crystals (black arrows) are clearly visible in the intercellular spaces near the vascular bundle (A) and interspace of mesophyll [(B), yellow arrows]. (C) - The presence of silicon in the cell walls of the upper epidermis, including in the guard cells of the stomata. (D) - The presence of silicon in the cell walls and into cells of the collenchyma near vascular bundle (arrows)
Histochemical staining of silica body in *T. angustifolia* leaf blades was carried out with methyl red and crystal violet lacton, whereas Si appears from light yellow-orange to a bright red color. Scale bar 50 µm.

Silicon content in cell walls, cytoplasm, and vacuoles is generally stable, even after plant destruction (Lins *et al.*, 2002). During vegetative growth, the silicon content of the plant changes (Voronkov *et al.*, 1978; Ma and Yamaji, 2015). This is shown on the horsetail (*Equisetum sylvaticum*), with the total silicon content increasing from 3.1 to 4.2% in the above-ground parts of the plants. From June to August inclusive, the organic silicon content decreased by 0.5%, the soluble silicon content almost halved (from 30.2 to 11.3%), while the polymer silicon content tripled (from 11.8 to 33.3%) (Kolesnikov, 2001). Early research on the leaves of *Melissa officinalis* and *Polygonum patulum* have shown that silicon binds not only to proteins and lipids, but to cell wall lignin (0.4 to 0.7%) and pectin (3.5 to 7.1% of total lignin in cells). The most common content of silicon associated with organic substances was about 50% of the total silicon content of the plant; e.g., in horsetail and trefoil it was about 0.3-2.3% of the absolute dry mass, while the proportion of silicon varied from 47.4% (in leaf clover) to 89.1% (in leaves of young grass, *Elytrigia repens*). In other species, the content of soluble silicon was also high and ranged from 3.3% (*Juncus acutiflorus*) to 11.2% (*Equisetum sylvaticum*) of the total silicon content. Polymer forms of silicon can make up from 6.0% (*Elymus repens*) to 33.8% (*Equisetum hyemale*) (Kolesnikov, 2001).

Silicon can deposit in leaf epidermis trichomes, giving these structures hardness and rigidity, making the leaves inedible to animals (Epstein, 2009). As a rule, most silicon is contained in cell wall protopectin, a water-soluble pectin fraction. Protopectin binds 1.9-6.8% of the total content of bound silicon, which was 0.01-0.09% of the dry leaf mass (in the *Polygonum patulum*). In addition, silicon has been found to strengthen cell walls and provide mechanical support to plants, as well as intensify the process of suberization, lignification,

and lead to the formation of a lot of silica cells (Guerriero *et al.*, 2016). In leaves content of silicon is dependent on cell type and type of tissue. Research established that the highest amorphous silicon content was found in trichomes, stomata and epidermal cells situated above the vessels in the leaves of *Phragmites australis* that grew in water and on terrestrial soil (Figure 3A and 3B) (Nedukha, 2018). Si content in plant cells is also dependent on soil moisture: in the leaves of terrestrial ecotype the Si content varied from 18 to 38 % (mass %), whereas in the leaf epidermis of *Ph. australis* grown in water the content of Si was significantly lower (Figure 3C and 3D). Using another method - laser confocal microscopy, the researchers found that the epidermis contained both amorphous and crystalline silicon (Figure 4A-F); in the amorphous state there were the particles smaller than 10 nm. Si can be in the crystal form of different size, from 5 to 10 μm (crystal facet) (Nedukha, 2018; Nedukha and Kordyum, 2019). The use of the program Pascal at laser confocal microscopy makes it possible to establish the differences in the luminescence intensity of silicon, or rather the number of photons that absorb silicon in different cells (Figure 4G and 4H) (Nedukha, 2018).

The presence of silicon is also shown by other researchers in prickly hair of epidermis leaves of *Deschampsia caespitosa* from different habitats (Grasik *et al.*, 2020). These authors have not observed correlation between leaf silicon content in the leaf, plant and soil. It has been shown that silicon was found not only in epidermal cells, but also in leaf mesophyll (Lins *et al.*, 2002). These investigators had shown the presence of spherical silicon bodies in leaf cells of *Syagrus coronata*: in vacuoles, in cell walls of mesophyll, and also in cell walls in the leaf hypodermal layer of *Syagrus coronata* using the scanning electron microscopy. Globular subunits with sharp edges formed the spherical silicon bodies that ranged from 6 to 10 μm in diameter. X-ray microanalysis detected the presence of silicon and oxygen homogeneously distributed throughout the Si-bodies (Lins *et al.*, 2002).

The presence of silicon inclusions in cytoplasm, vacuoles and vesicles of mesophyll cells by an electron microscopical method was observed in leaf cells of *Nicotiana tabacum*, *Arabidopsis thaliana*, *Silene vulgaris*, *Cardaminopsis halleri*, *Minuartia verna*, *Armeria martitima*, *Viola calaminaria*, *Thlaspi caerulescens*, and *Cardaminopsis halleri* (Neumann and De Figueiredo, 2002; Neumann, 2003). Vacuoles of mesophyll cells contained a large number of silicon granules ranging from 20 nm to 1.2 μm in size. Transmission electron microscopy associated with electron spectroscopic imaging used to determine the elemental composition of the granules. Si-granules in vacuole were amorphous and composed of silicon and oxygen too (Lins *et al.*, 2002). The particular importance is the fact that these researchers identified silicon crystals in the intercellular spaces, between the cell wall and the plasma membrane, and into the vacuole near tonoplast. Many of these Si-inclusions show the presence of electron dense borders along the periphery of crystals. The authors proposed the scheme of silicon transport from apoplast both by endocytotic vesicles into vacuole and from apoplast across plasma membrane into cytoplasm and then to vacuole.

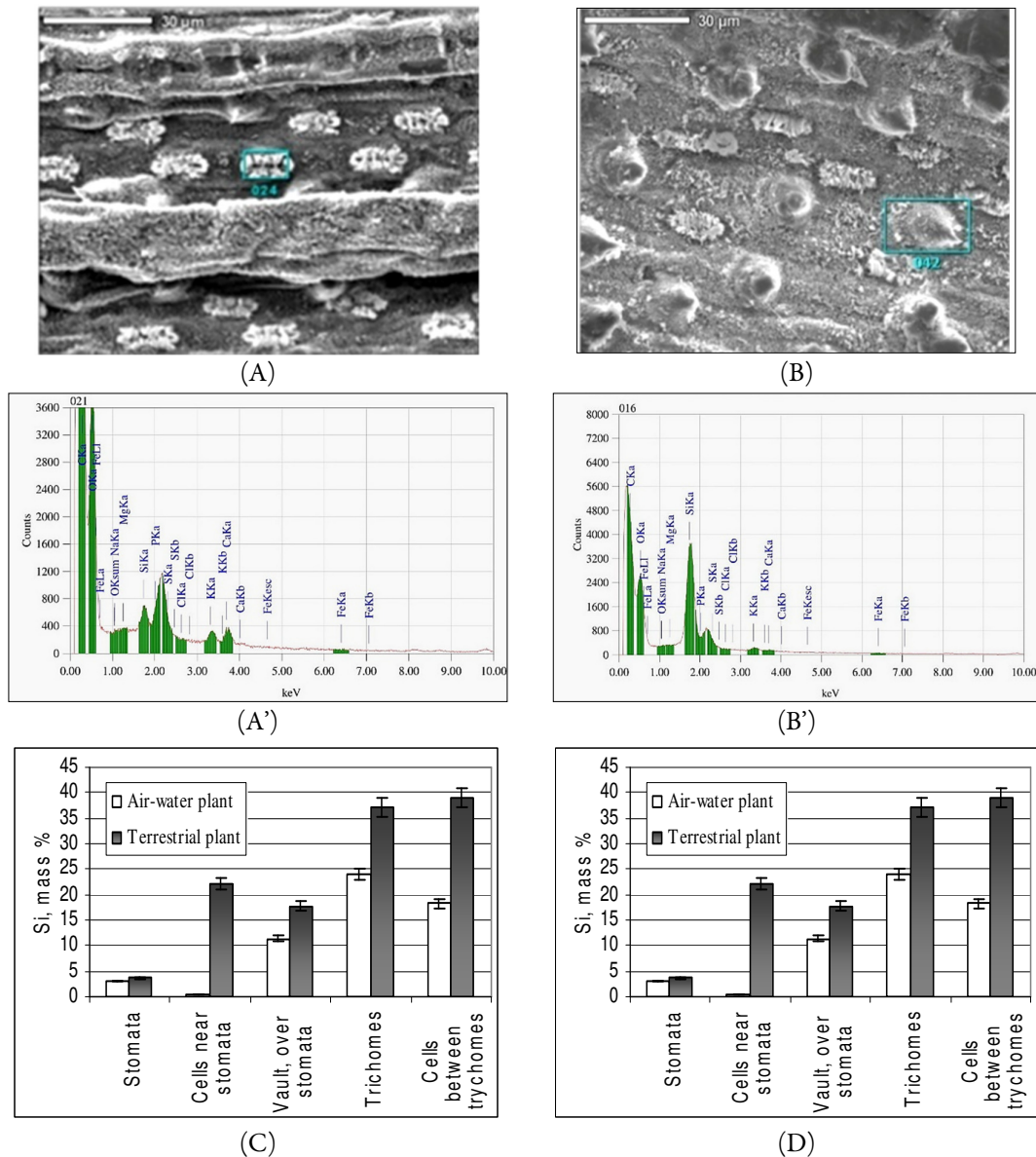


Figure 3. Micrographs of epidermal cells (stomata and trichoma) with spectra of Si and other chemical elements measured by X-ray technique in leaf *Phragmites australis* air-water (A) and terrestrial (B) plants. On the upper part of each figure, outlined in the green square is the cell of epidermis surface that was scanned by X-ray method. At the bottom of each figure (A) and (B) is the histogram (A' and B') of the content of chemical elements, including silicon; the axes: Y-axis showed as counts per second (cps), notably impulses eV per second; X-axis showed energy in keV (kilo-electron volts). (C) and (D) - Silicon content (mass %) in the leaf cells of adaxial (C) and abaxial (D) epidermis *Ph. australis* air-water and terrestrial plants investigation was obtained with X-ray analysis (Nedukha, 2018)

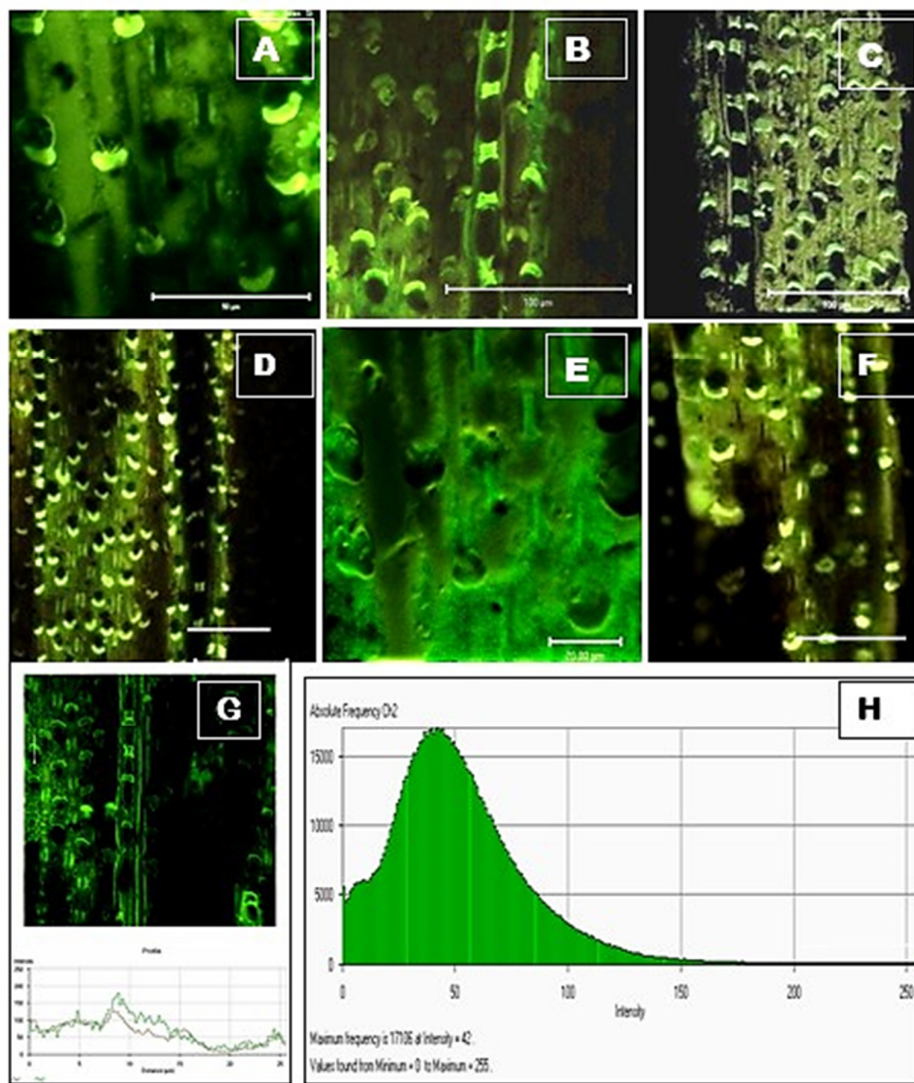


Figure 4. Confocal microscopy analysis of fluorescence of silicon (Si) in leaf cells of *Phragmites australis* air-water (A, B, C, D) and terrestrial (D, E, F) ecotypes at vegetative stage. Localization of Si has green fluorescence. Epidermis types are noted: (A, B, D, E) – adaxial surface; (C) and (F) – abaxial surface; (G) – histogram of fluorescence intensity of Si (green line). Ordinate – Fluorescence intensity, relative units; abscissa – distance (μm), which was scanned on the figure; this distance is shown as while lining on Si-crystal structure or Si-amorphous structure. (H) – Absolute frequency of pixels for Si (green graph). Scale bars: 50 μm (A, D, E), 100 μm (B, C); 20 μm (E). Laser confocal microscopy. (Nedukha, 2018)

Plant cells are used as an analogous transport to remove heavy metals (Neumann and De Figueiredo, 2002). Root cells serve not only for the absorption of silicic acid from the soil to above-ground organs, but they also accumulate silicon, especially in cell walls, like to leaf cells. It was established that in rice roots, silicon enhances synthesis of suberin and lignification of tissues. It was shown that the total content of mineral silicon in the roots is greater than in the aboveground organs. The portion of organic-bonded silicon was about 34.0-36.6% of its total content (*Festuca pratensis*), given the fact that an accumulation of mineral forms of silicon in the roots was very big (Kolesnikov, 2001; Suzuki *et al.*, 2012). And thus, Si activates the development of endoderm tissue and cells of exoderm Casparian strip. This was established in rice, maize and onion (Fleck *et al.*, 2015). Despite numerous studies on the presence of silicon in cultivated and some wild plant species, there

is a gap in the study of silicon's role and participation. in preserving certain eco-system. In our opinion, promising investigate the silicon content in the leaves of trees that are resistant to drought and the action of dry winds, which will have a positive effect in the study of ecosystem tolerance and biodiversity formation.

Functions of Silicon

Regulation of water balance

It is known that stomata and cuticles of epidermal leaf walls take part in maintaining the optimal water balance of cells. The rate of cuticle transpiration can vary significantly depending on the density and size of the cuticle pores, the composition of the cuticle, the plant growth phase and the influence of environmental factors (Kerstein, 2006; Schönher, 2006). It has been established that silicon affects the cuticle transpiration of aboveground organs. This chemical element, which accumulates in the cells of the epidermis of leaves and stems, forms a double thickened cuticle-silicon wall, which protects the plant from excessive moisture consumption, by reducing the cuticle transpiration. In addition, the plants' cells can form hydrophilic silicate-galactose complexes that bind free water, thereby increasing the water retention capacity as in specific cells, as and in different tissues and in the plant. Because of the density of cell walls and their ability to retain moisture, silicon compounds can significantly increase plant resistance to drought and protect plants from being lodged (fallen) (Hodson *et al.*, 2005). Silicon reduces of water evaporation on the leaf surface, as has been shown, for example, on rice seedlings (Ma and Takahashi, 1993). Similar effects have been found on other crops, in particular in drought-resistant wheat (Gong *et al.*, 2005) and sorghum (Hattori *et al.*, 2008; Ahmed *et al.*, 2011). Silicon can also influence water transport by regulating the osmotic potential of cells by increasing synthesis and accumulation of osmotic active substances (e.g., proline, sugars and inorganic ions) (Pei *et al.*, 2010; Ming *et al.*, 2012; Liu *et al.*, 2014;). At the same time, Si did not affect transpiration in cucumbers (Hattori *et al.*, 2008). Such features may be related to differences in the peculiarities of structure and functions of epidermal cells of the species. The mechanisms underlying these differences require further investigation.

Regulation of sun light absorption

Silicon takes part in the regulation of the absorption of sun light by the leaf surface. It improves luminous flux characteristics of absorption light by holding the rolled-up leaves and thus promotes the photosynthetic process (Ma *et al.*, 2011; Mirshafieyan and Gue, 2014). According to physicists who have studied the optical properties of silicon, it has been found that Si can absorb light in a wide range (from infrared to ultraviolet) very quickly, it with about 1017 photons per cm² per second, and respectively 1.12 eV (Würfel, 2009; Nor Afifah Yahaya *et al.*, 2013; Mirshafieyan and Guo, 2014). Wavelengths (nm) of silicon absorption range from 450 to 1100 nm (Yahaya *et al.*, 2013; Loiko and Miskevich, 2015). It is calculated that the ideal absorption and reflection of light by silicon occurs when its thickness varies from 110 to 140 nm, i.e. it is the optimal thickness of silicon inclusions (Hofmeister *et al.*, 2009). It is established that in the amorphous state (not in the crystalline) silicon absorbs light best, because amorphous silicon is tetrahedral structure and it is characterized by specific shorter order as crystalline silicon, the coordination number is close to four, interatomic distance in α -Si differ from corresponding crystalline values by several percent and actuations of tetrahedral angles are about 10° (Figure 1A) (Kolesnikov, 2001). It was found that the onset of strong absorption of light by silicon occurred when other particles or ions attach to silicon (Loiko and Miskevich, 2015).

According to Wang *et al.* (2005) silicon epidermal cells reduce the influence of thermal effect on the leaves by reflecting the heat flow in the far infrared region of the sun light flux. This provides a passive mechanism for cooling the leaves in high sunlight, although the mechanism of this action is not yet known, so that these issues need further study. Given the above, it can be argued that the presence of amorphous silicon inclusions in the epidermal cells of the leaves optimizes the absorption and reflection of light by the leaf surface for the survival of the plant in an environment of significant sunlight intensity.

Involvement of silicon in protecting plants from the effects of toxic metals and semi-metals

Modern industrialization and urbanization influence pollution of the environment by contaminating soils and water sources with heavy metals and semi-metals, which can be destructive to the ecosystem. However, plants have elaborated survival mechanisms under such conditions. Reactions of plants to abiotic stress include activation of reception and signal transduction systems, further activation of protector systems, in particular, antioxidant and stress protein synthesis systems, which are involved in adaptation to stress factors of different nature, i.e., are non-specific (Kolupayev, 2001; Kosakivsky, 2003; Kolupayev and Karpets, 2010; Belyavskaya *et al.*, 2018). In addition to participating in the activation processes of non-specific plant protection systems, silicon can reduce the toxic effects of chemical elements. In particular, Si situated in soil, immobilizes toxic metal and semi-metal ions such as aluminum (Al), arsenic (As), cadmium (Cd), iron (Fe), manganese (Mn), and zinc (Zn) by formation of complex ions, eventually removing them from the rhizosphere as insoluble precipitation (Liang *et al.*, 2005; da Cunha *et al.*, 2008; Naeem *et al.*, 2014). For example, silicon that forms complexes with Al, which forms inert hydroxyl-alum silicates in the soil solution and thus reduces the toxicity of Al (Li *et al.*, 1996; Liang *et al.*, 2007). In corn, silicon stimulates the removal of phenolic compounds from the roots, which form complexes with Al ions, and reduces their absorption by the roots (Wang *et al.*, 2004).

The increased silicon content in the soil reduces absorption and further accumulation of Al in rice stems. It has been shown that exogenous application of Si increases soil pH and reduces the solubility of chemical elements and, consequently, the action of toxic metals to the plant root system (Ma *et al.*, 2008). It is known that plant silication associated with the polymerization of silicic acid into the cell apoplast leads to the formation of an amorphous silicon barrier (Exley, 2009), which prevents the penetration of potential toxic ions such as aluminum, manganese, cadmium, and zinc to plant (Fleck *et al.*, 2015).

Protective effect of Si at salinization and drought

The effects of drought have much in common with the effect of salinization on plants. Soil salinization occur about one-third of all agricultural land and almost half of all irrigated land that produces about one-third of the world's food (Zhu, 2001). The positive effect of silicon on plants when soil salinization occurs is through the strengthening of ion pumps involved in transporting sodium from cytoplasm to vacuole, by activating the H⁺-ATPase tonoplast and cytoplasmic membrane (Rizwan *et al.*, 2015; Hamam *et al.*, 2016). It is known that when salinized, lipid peroxidation of membranes (POL) increases in cells (Gill and Tuteja, 2010) and silicon reduces the content of malonate dialdehyde, which is the end product of POL. In particular, this is due to the activation of antioxidant enzymes such as superoxide dismutase, peroxidase and glutathione reductase under Si influence, which leads to increased plant resistance in saline conditions (Liang *et al.*, 2006; Shi *et al.*, 2016). The treatment of seeds before sowing with silicon compounds for a short time (6 to 12 h) also affected germination rates and increased the content of photosynthetic pigments, sugars and soluble proteins, resulting in higher yields under saline soil (Ahmed *et al.*, 2016; Latef and Tran, 2016).

Drought is even more common and damaging to agricultural production, especially in dry and semi-arid regions (Farooq *et al.*, 2009). One of the mechanisms of resistance and plasticity of the plant to drought is the synthesis of stress proteins, one of which is dehydrin protein, whose activity is increased by silicon (Chen *et al.*, 2008; Wang *et al.*, 2008). Dehydrins are high-hydrophilic proteins belonging to LEA group (Late Embryogenesis Abundant) proteins, typical for the late phase of embryogenesis, when there is a natural dehydration of ripening seeds. LEA proteins interact with cell structures, preventing their degradation during cell dehydration. It is believed that the synthesis of these proteins is controlled by the phytohormone abscisic acid (ABA). Such proteins synthesize not only in seeds, but also in vegetative organs of plants during abiotic stress and these proteins can be used as stress markers of adverse conditions on plants (Hudertmark and Hinch, 2008; Ling *et al.*, 2016). The functions of these proteins have many-sides: chaperone, cryoprotective, antifreeze, radical-binding and ion-binding. LEA proteins influence changes in the thermodynamic of protein-water interaction and thus provide stability of proteins and nucleic acids during cell dehydration (Rotat, 2006).

Silicon has also been shown to reduce or stop oxidation processes that can lead to cell damage (Takasaki *et al.*, 2010; Song *et al.*, 2011); silicon can also activate the genes (particularly *OsRDCPI*) responsible for the synthesis of glycine-betaine osmotic substance, which is important for resistance to drought and salinity (Khattab *et al.*, 2014). Plant silication, which is associated with the polymerization of silicic acid in the apoplast, leads to the formation of an amorphous silicon barrier (Exley, 2009), which increases the binding of sodium with the cell wall of the roots, while reducing the transport of sodium ions to the stem under saline conditions (Ahmad *et al.*, 1992; Saqib *et al.*, 2008). Silicon is also known to influence the synthesis and accumulation of polyamines, such as putrescine, spermidine and spermine, which have direct and indirect antioxidant effects and modify osmotic potential, and thus increase resistance to adverse environmental factors, including soil salinization (Kusano *et al.*, 2008; Yin *et al.*, 2016). It is known that increased expression of the genes responsible for polyamine synthesis can attenuate of the negative effects of oxidative stress, drought and soil salinization (Tang *et al.*, 2007).

The effect of silicon on polyamine synthesis was studied on sorghum plants (*Sorghum bicolor*) (Yin *et al.*, 2016). The increase in Si increased the expression level of the gene of S-adenosyl-L-methionine decarboxylase (SAMDC), involved in the synthesis of polyamines, and in the suppression of ethylene, which competes with polyamine for the common precursor-S-adenosyl-L-methionine (SAM) (Pandey *et al.*, 2000). Polyamines are also involved in various vital processes such as replication, transcription and translation (Tabor and Tabor, 1984; Roy and Wu, 2001). Thus, activation of polyamine biosynthesis that is occurred with silicon reduces the effects of stressors and promotes plant growth and their development in the condition of soil salinization.

The study of the ameliorative effect of silicon from *Melia azadirachta* leaf and sugar beet was investigated on salinity-induced detrimental effects in *Pisum sativum* (Shahid *et al.*, 2015). Exogenously applied Si and phyto-extracts markedly alleviated the salinity-induced drastic effects on growth, gas exchange attributes, and productivity. Both phyto-extracts supplemented with silicon gave highly salinity mitigating effects by markedly improving growth, gas exchange attributes, enzymatic activities, osmolytes, and yield. These authors have shown that exogenous application of silicon in combination with phyto-extracts of *Melia azadirachta* and sugar beet was a highly effective ameliorative approach to alleviate salinity-induced hazardous effects in plants, especially in pea, grown under a saline regime.

The data indicate that further studies of silicon's participation in the adaptation and the planting in natural communities and agrocoenosis, forest and steppe vegetation under current conditions of anthropogenic influence and prediction of global climate change are promising.

Protective effect of Si at pathogens invasion

It is known that Si plays a positive role in plant–pathogen interactions; it increases plant resistance to disease caused by fungi, bacteria, viruses, and nematodes (Cherif *et al.*, 1994; Fawe *et al.*, 1998; Bockhaven *et al.*, 2013; Wang *et al.*, 2017). During a pathogen invasion of plant, the epidermis of leaves, stems, and roots, in the presence of silicon in external (periclinal and anticlinal) cell walls, protects the plant from penetration of pathogenic microorganisms and fungi (Brenchley *et al.*, 2008). If the pathogen has partially destroyed the epidermal cell of the plant and penetrated into the cell-host, the protection against the pathogen occurs both in this cell and in neighboring cells surrounding the cell occupied by the pathogen. Activation of lignin synthesis and silicon bio mineralization was observed in intact cells adjacent to cells invaded by the pathogen for mechanical strengthening of cell walls, which are the defensive boundary against the action of pathogens (Rodrigues *et al.*, 2003; Wang *et al.*, 2017). This occurs similarly to events under abiotic stresses (drought and salinity) involving silicon (Suzuki *et al.*, 2012). Whereas in the cells into which the pathogen penetrates, other events occur: harmful effects of biotic stress due to a number of mechanisms, including the synthesis of antibacterial and antifungal compounds and provokes a broader response to pathogenic attack, which events lead to cell-host necrosis (Menzies *et al.*, 1991; Cherif *et al.*, 1994). For example, in early studies on the pathogenesis of rice by *M. grisea* or *Pyricularia oryzae* a decrease in the degree of invasion in the epidermis and

mesophyll cells was established. This process was accompanied by an increase in the content in flavonoids, ferulic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, and vanillin acid in these cells (Ohata *et al.*, 1963; Suzuki, 1965). Correlation between the phenol content and polyphenolase provided a convincing argument that the production of phenols at a low concentration within and around the infection sites delayed the necrotic response to the infection by *Magnaporthe grisea* pathogen (Suzuki, 1965).

In later works, it was proven that silicon-induced resistance to powdery mildew caused by *Podosphaera xanthii* in cucumber plants (Fawe *et al.*, 1998), to powdery mildew in wheat and rice (Wang *et al.*, 2017), and *Magnaporthe grisea* in rice seedlings (Rodrigues *et al.*, 2003), was explained by increased synthesis and accumulation of antifungal compounds phytoalexins and other phenolic and flavonoid substances. Phytoalexins are antimicrobial and often antioxidative substances synthesized *de novo* by plants that accumulate rapidly at cells of pathogen infection. Several classes of phytoalexins are known: terpenoids, glycol steroids and alkaloids, which act as toxins to the pathogen organism.

Phytoalexins, which act as toxins for the attacking pathogen can puncture the wall of cell-host, delay maturation, disrupt metabolism or interfere with the reproduction of the pathogen. Their importance in plant protection indicates an increase in the susceptibility of plant tissue to infection by inhibiting the biosynthesis of phytoalexin (Darvill and Albersheim, 1984; Glazebrook and Ausbel, 1994). Since rice is one of the main food crops for many people in the world, most studies on the impact and pathogens on this culture have been conducted on rice. It's proven that resistance of rice to numerous pathogens, including blast, brown spot (*Cochliobolus miyabeanus*), stem rot (*Magnaporthe salvinii*), leaf scald (*Monographella albescens*), sheath blight (*Thanatephorus cucumeris*), and grain discoloration (Datnoff *et al.*, 1997; Seebold, 1998; Rodrigues *et al.*, 2003) was mediated by the influence of silicon on the production of a protective reaction of the cell-host. In many cases, Si can control rice blast as effectively as recommended fungicides.

It is shown that the proteins involved in the activation of the synthesis of secondary metabolites of phenylpropanoid pathway with silicon participation operative very actively (Cherif *et al.*, 1994; Datnoff *et al.*, 1997; Remus-Borel *et al.*, 2005). In addition, silicon deposits at the site of a pathogenic attack also reduce of the damage to the cell-host epidermis by fungi or bacteria due to increased strength of cell walls in plant epidermal tissues (Rodrigues *et al.*, 2003). Experiments performed on cucumber leaves shown that further resistance to infection is acquired by the expression of a proline-rich protein together with the presence of silica at the site of attempted penetration. The C-terminal end of this protein contained of lysine and arginine residues that are possessed of deposition of silica at the site of vulnerability. This protein is analog of the composition of the R5 peptide found within the silica of some diatom algae (Perry and Keeling-Tucker, 2003). Addition of Si to soils significantly reduces the range of biotic stress symptoms. The use of silicate-containing fertilizers in agriculture is increasingly practiced to improve plant productivity by reducing negative stress exposure (Datnoff *et al.*, 2001). In concluding this section, it is considered that the conceptual basis for the protection and preservation of plants from abiotic and biotic stresses can be the addition of silicon in soil, while for the conservation of agrocenosis, forests and steppe vegetation in the face of global warming of climate requires the preservation and reproduction of species characterized by increased silicon absorption and accumulation of silicon in the leaves and stems. The latter proposal and recommendations require a far-reaching joint study of ecologists, agronomists, foresters and multidisciplinary biologists.

Participations of Si in the plants' molecular mechanisms of growth and adaptation t stress

Silicon-dependent gene expression was first investigated on rice seedlings. According to the results, the addition of Si in plant growth medium influenced the expression of the gene (*Cha21*) of the protein homologue carbonic anhydrase associated with the synthesis of chlorophyll *a* and *b* (Watanabe *et al.*, 2004). Later, Song *et al.* (2014) showed the participation of silicon in regulating the expression of genes associated with photosynthesis under conditions of toxic action of zinc. At molecular level during a real time RT-PCR, during investigation on the beneficial effect of Si (1.5 mM for 7 days) on Zn toxicity in *Oryza sativa* cultivar grown hydroponically, was established the enhanced activity of the *PsbY* (polyprotein of photosystem II, PSII) activity

and improved behavior to Zn stress (Song *et al.*, 2014). The addition of Si increased the level of the transcript *PsbY* (*Os08g02630*), while Zn in high concentrations slowed down the expression of this gene (Kawakami *et al.*, 2007). In addition, silicon affected the expression of the *PetC* gene (Song *et al.*, 2014), associated with cytochrome's biological processes in photosynthesis (Breyton *et al.*, 1994).

Early, it was shown that in the absence of *PsbY*, the mutant did not affect the composition of PSII and the growth of photoautotrophic algae (Funk, 2000). However, tests proved that *PsbY* was a manganese-binding polypeptide with L-arginine metabolizing enzyme activity, pointing to the possible role of this subunit in the function of the Mn₄Ca-cluster in oxygen-evolving PSII (Gau *et al.*, 1998; Kern *et al.*, 2010). In the experiments on rice, Song *et al.* (2014) established that the relative gene expression level of *PsbY* increased with the addition of Si under high-Zn stress, suggesting that the manganese-binding capacity was increased, and water oxidation was enhanced in the PSII of rice. These results showed that the addition of Si in the medium could induce the rapid expression of the *PsbY* gene in rice, a gene that has a novel manganese-binding, low-molecular-mass protein associated with PSII. Silicon also activated other chloroplast genes, namely *Os03g57120* and *Os09g26810*, which are involved in the light-gathering complex associated with photosystem I and photosystem II, i.e., silicon decreased chlorophyll degradation under abiotic stress (Song *et al.*, 2014).

It is known that certain transcription factors (TF), which are the main regulators of genes, participate in the formation of protective reactions of plants (Gao *et al.*, 2007). It was found that even one TF can control the expression of target genes by specific binding of TF to cis-acting element in the promoters of corresponding genes under the action of abiotic stress (Umezawa *et al.*, 2006; Nakashima *et al.*, 2009). Such expression of target genes is significantly increased with the participation of silicon ions (Wang *et al.*, 2008; Mizoi *et al.*, 2012; Khattab *et al.*, 2014). Rice plants have shown that silicon increased the expression of genes of *DREB2A* (dehydration-responsive element binding protein), choline monooxidase (*OsCMO*), and dehydrins proteins (*OsRAB16b*), which ensure drought tolerance of rice (Chen *et al.*, 2008; Wang *et al.*, 2008) and the plant's resistance to oxidative stress, and as a result, these proteins generally protected the plants for droughts. Silicon has also been shown to influence the expression of stress genes responsible for the synthesis of LEA3 proteins in rice plants (Takasaki *et al.*, 2010). As already noted, these proteins protect cell structures during dehydration caused by stressors of different nature (Lenka *et al.*, 2011).

According to molecular biology studies, the gene responsible for the synthesis of protein - transporter Lsi1, which transports silicon into the cells of the endo- and exoderm of the roots, contains five exons and four introns and encodes protein, consisting of 298 amino acid residues. This protein is very similar to the homology of aquaporins, including six transmembrane domains and two domains with pro - ala motives. Protein Lsi1 is constitutive (Ma and Yamaji, 2006). It was also found that the expression of the genes responsible for the synthesis of E1, E2 and E3 ligases involved in plant drought adaptation was amplified with the participation of silicon (Manivannan and Ahn, 2017). The enzyme choline mono oxygenase is the primary enzyme that participates in the biosynthesis of osmotic protein - glycine-betaine. Thus, the Si-frequently activates the expression of *OsCMO* genes that increases the dehydration resistance of rice (Burnet *et al.*, 1995). Silicon is also involved in the regulation of gene expression of proteins participating in phenyl-propanoid cycle (Manivannan and Ahn, 2017).

Molecular mechanisms of silicon influence have been established during the study of plants' responses to the pathogen damage. It is revealed that silicon activates the genes of chalcone synthase, phenylalanine amoniliase, peroxidase, callose-synthase (β -1,3-glucanase), and chitinases (Fauteux *et al.*, 2005). This activates the plant protect mechanisms of pathogen damage, while strengthening the cell walls of the host-plant. In addition to activating the phenylpropanoid pathway, Si can influence plant resistance to pathogen invasion by regulating the genes involved in hypersensitivity reactions and jasmonic acid-dependent processes (Rodrigues *et al.*, 2003; Watanabe *et al.*, 2004; Wang *et al.*, 2017). Cellular and molecular mechanisms of action of Si, which activates the expression of stress proteins genes and enzymes involved in the synthesis of osmotically active substances and various secondary metabolites, have been established on agricultural crops and wild

species. The participation of silicon in the processes of strengthening cell walls is of special importance for plant stability.

Conclusions

The results of numerous studies indicated that silicon in the form of silicic acid is transporting from the soil to the root, through the exoderm, endoderm and xylem of the root and then to above ground organs. Progress on this issue is the discovery of some of the transporter proteins involved in the process. Protein transporters of silicon (*Lsi1*, *Lsi2*, *Lsi6*) in different plant species were revealed. However, the regulation of gene expression of these proteins is species and tissue-specific and the question of the mechanism of regulation of such transport-proteins remain open.

Previous data shown that dioxide silicon can locally associate with polysaccharides, proteins or other substances in root cells, stem and leaf. The content of accumulated amorphous or crystalline silicon in a plant cell depends on the growth stage and environment. It was established that the intensity of absorption of sunlight and photosynthesis, transpiration rate, water balance of cells, and the mechanical properties of cell walls are due to the accumulation of silicon in the cell walls of the epidermis. The question of the functioning of crystalline silicon deposits in the intercellular spaces and in the vacuoles of cells is open.

Numerous studies have established that silicon activates the protective systems of plant under the action of adverse abiotic factors (drought, salinization, an action of heavy metals and semi-heavy metals) and pathogen invasion too. The mechanism of this action is due to the activation of dehydrins, osmotic substances (glycinebetain) and polyamines, which change the osmotic potential of cells. Silicon reduces the content of malonic aldehyde, weakening POL in cells. Under biotic stress conditions, silicon activates the synthesis of phytoalexins and enhances the mechanical properties of the cell walls of the host-cell. The primary mechanism of action of silicon in the pathogenesis also remains open.

Thus, the obtained information indicates the prospects of further studies of silicon participation in plant adaptation to adverse changes in environmental factors in natural communities and agrocoenosis in modern conditions of increasing anthropogenic pressure and forecast of global climate change.

Authors' Contributions

The author read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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