Silicon, the Long Forgotten Element of Plants

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Zusammenfassung

Silizium (Si) hat positive Auswirkungen auf die Pflanze und ermöglicht ihr eine wesensgemässe Entwicklung, unabhängig davon, ob sie Kiesel (SiO_2) speichert oder nicht. Das wird hier durch die Ergebnisse neuerer physiologischer Untersuchungen belegt. SiO_2-Ablagerungen finden sich an der Peripherie der Zellen und Organe der Pflanze; sie werden durch eine Matrix ermöglicht, die aus Zuckerpolymeren oder aus Proteinen besteht, deren Struktur ähnlich der des Kollagens ist. Die SiO_2-Ablagerungen nehmen mit dem Alter der Pflanze zu, im Gegensatz zu ihrem beobachteten Vorkommen in menschlichen Geweben. Silizium kann in der Pflanze alternativ Funktionen von Ligninen oder Zellulose übernehmen und somit hinsichtlich physiologischer Aufgaben den Kohlenstoff ersetzen. SiO_2 bewirkt einen Lichteffekt, der generell die Leistung der Photosynthese und die Entwicklung der Pflanze fördert. Kiesel wirkt antagonistisch zum Kalzium sowie auch zur Wirkung von Stickstoff, die nach Rudolf Steiner beide Träger der Astralität sind. Kiesel kann unausgewogene Nährstoffverhältnisse im Boden ausgleichen und lindert die Belastung der Pflanze durch biotischen wie auch abiotischen Stress. Diese aktuellen Daten bestätigen die Beschreibungen und Anregungen Steiners, die in der biodynamischen Landwirtschaft eingesetzt werden.

Summary

Silicon (Si) has a positive effect on plant development and growth, and enforces outward expression of its inner nature, regardless of whether the plant stores silica (SiO_2) or not. This positive effect is demonstrated here by the results of recent physiological studies. SiO_2 deposits are found on the periphery of plant cells and organs, in a matrix made up of sugar polymers or proteins whose structure is similar to that of collagen. SiO_2 deposits increase with plant age, as opposed to a decrease in human tissues when ageing. Silica can alternatively take over functions of lignins or cellulose in the plant and thus replace carbon with regard to physiological tasks. Moreover, SiO_2 causes a light effect which generally promotes the performance of photosynthesis and the development of the plant. Silica acts antagonistically to effects of calcium as well as nitrogen, which according to Rudolf Steiner, are both carriers of astrality. Further, Silica can balance nutrient conditions in the soil and reduce biotic and abiotic stress on the plant. These current data confirm Steiner's descriptions and suggestions, which are used in biodynamic agriculture.

Résumé

Il est démontré que le silicium (Si) est un élément bénéfique, voire crucial pour la plante, qui permet de préserver l'expression de son génie, qu'elle soit accumulatrice ou non. Les dépôts de silice (SiO_2) sont observés en périphérie des cellules et

des organes de la plante; ils sont rendus possibles par une matrice constituée de polyolates ou de protéines de structure apparentée à celles du collagène. Les dépôts de SiO_2 augmentent avec l'âge, contrairement à ce que l'on observe chez l'homme. Le silicium est une alternative à la lignine ou à la cellulose : ce que fait le silicium, le carbone n'a plus à le faire. La SiO_2 agit par son effet lumière et globalement améliore l'efficacité de la photosynthèse et le développement de la plante. La SiO_2 est antagoniste de calcium et des effets de l'azote, deux éléments support de l'astral. La SiO_2 corrige les déséquilibres nutritionnels et atténue les stress biotiques et abiotiques. Ces données récentes confirment les descriptions et les propositions de Steiner, mises en œuvre par l'agriculture biodynamique.

Overview

Silicon does not exist as a free element anywhere in nature. It is present everywhere in the form of silicates, silica or silicic acid in rocks, soil, but also at low or very low concentrations in water and in the atmosphere. For the most part (90%), the earth's crust and soil consist of silica and silicates; silica alone comprising 50%. Note that silicon is completely black and opaque. On the other hand, silica, the product of silicon's reaction with oxygen, is a kind of white or colourless ash that is transparent to light. Silica is a very hard solid body; it is a receptor and transmitter of light (*Steiner* 1924; *Benesch & Wilde* 1983).

Silicon (*Si* in the following)[1] is present in all plants (0.1 to 10% of dry weight) (*Hodson et al.* 2005). The silicon content varies according to the nature of the soil, the season, the plant's phenophase, the species and the genotype of the same species. Generally speaking, silicon is one of the most abundant mineral elements in plant tissues: the concentration of 0.1% is identical to those of the most important elements such as phosphorus, sulphur, calcium and magnesium (*Epstein* 1994).

Taking into account the ratio of silicon to calcium concentrations, plants have been classified as accumulative, moderately accumulative or non-accumulative. Some of them, such as Fabaceae or tomatoes, even appear to partially reject *Si* (*Ma* 2001; *Liang et al.* 2007; Nikolic et al. cited by *Shi et al.* 2014)[2]. It has been shown that primitive plants such as liverworts, mosses,

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[1] *Si* means silicon in the form of silica (SiO_2) or silicic acid ($Si(OH)_4$), unless the context indicates to the reader what form it is.

[2] In former literature, the term "silica process" is mentioned for plants considered as devoid of *Si* according to results obtained by old analytical methods. But to verify this hypothetical concept, old test results should be corroborated using modern methods such as inductively coupled plasma spectrometry (ICP-AES) which is approximately 500 times more sensitive than traditional colourimetric methods (detection limit about 20 µg / L) (*Misund et al.* 1999).

lycophytes and equisetophytes among the spore-formers and primitive dicotyledons accumulate more silicon than the more recent plants such as polypodiophytes (ferns), gymnosperms and angiosperms. Among the latter, monocotyledons comprise strongly accumulative plant families such as the Poales (Graminae), Cyperaceae (Carex) and Arecales (palms). Among the dicotyledons, plants of certain taxa accumulate significant quantities, such as Urticaceae (cf. *Urtica dioica* = stinging nettle), Cucurbitaceae (*Cucumis sativa* = cucumber) and Boraginaceae (*Borago officinalis* = borage) (*Hodson et al.* 2005; *Curry & Perry* 2007).

Origin of silica

Long ago in the history of the Earth it was an amorphous mass, soft in consistency, denser and hotter in its centre. It was permeated from its periphery to its interior by the sun's rays. It was light of a semi-substantial lamellar nature, a kind of 'light-silica', simultaneously process and substance. These light-silica lamellae are organised in gigantic envelopes similar to the contours of huge crystals within which appeared the primitive plants. These fixed a small amount of silica in colloidal form. The silica separated from the light but remained completely transparent. At the end of each cycle following the death of these primitive plants, the silica was released into the surroundings, and, depending on the succession of cycles, accumulated to constitute the material for the formation of the continents (*Steiner* 1923; *Benesch & Wilde* 1983). This origination phenomenon finds its echo in the accumulation of phytoliths from dead plants in the soil. These phytoliths break down very slowly, therefore making it understandable that their study gives information on the flora of past geological eras, and that they may be of archaeological interest (*Hodson et al.* 2005; *Cooke & Leishmann* 2010).

Absorption, transport and distribution of silicon in the plant

The soil is the main source of mineral elements necessary for plant growth. The siliceous minerals consist mainly of aluminosilicates (1/3) and siliceous phytoliths (2/3), which come from dead plants (*Conley* 2002; *Cooke & Leishmann* 2010). Erosion, i.e. the permanent interaction between the solid elements and the gaseous and liquid phases of the soil, supplies the soil water with silicic acid, the absorbable form of *Si*. The living organisms of the soil biosphere (fungi, bacteria etc.) and plant roots interact with soil minerals and play an equally important part in *Si* solublisation. In soil water in contact with roots, silicic acid is largely present at concentrations between 0.1 and 0.6 mM, like most major mineral nutrients such as potassium, calcium and sulphates (*Epstein* 1994; *Hodson* 2005; *Yamaji et al.* 2008; *Currie & Perry* 2009, *Mitani et al.* 2011).

Si is absorbed by roots in the form of silicic acid. Mechanisms of silicon absorption and distribution have been studied in rice (Poaceae) (*Ma* 2009; *Ma et al*. 2011). Transporters designated by the acronyms Lsi1, Lsi2 et Lsi6 have been identified in lateral roots. Lsi1 and Lsi6 are membrane proteins of the aquaporin group which are selective but passive filters for water and certain weakly polar dissolved substances such as silicic acid. Their functioning is controlled by the mechanisms of osmosis. Lsi1 is located in the cortical part of functional lateral roots. It is responsible for the absorption of silicic acid from the soil. On the other hand, Lsi2 is an active transporter requiring energy for its functioning. It ensures the export of silicon into the xylem and maintains its concentrations in the root cortex at a low level so that passive absorption by Lsi1 can continue. After absorption, *Si* enters the xylem where it is present in the form of monosilicic acid, organic sap compounds preventing it from being deposited.

Lsi6 is localised in the parenchyma close to the xylem vessels. It is responsible for transfer of silicic acid to xylem and ensures its distribution in tissues (*Yamaji et al*. 2008).

Variants of these transporters have been identified according to species (rice, maize and barley), as well as different active or passive absorption mechanisms in plants other than Poaceae (*Yamaji et al*. 2008; *Epstein* 2009; *Ma* 2009; *Cooke & Leishman* 2011; *Mitani et al*. 2011; *Grégoire et al*. 2012). It is accepted that other *Si* absorption mechanisms exist as well as other unidentified transporters.

Cell wall composition

The wall is a more or less rigid structure primarily comprising cellulose (a branched-chain glucose polymer) that surrounds the cell. The primary cell wall of a young (active) cell is supple, extensible and permeable, allowing the cell to grow. The cellulose fibres that it contains are disordered, without any particular orientation. On the other hand, older walls, i.e. secondary walls, are definitive, rigid and impermeable structures whose cellulose fibres are orientated. This cell wall is more or less filled with lignin. The cell is dead. *Si* is an important component of the cell wall. It accumulated in the walls of cells that are still active, where it behaves as a crosslinking agent, strongly bound to polysaccharide components, and ensures the stability and structural robustness of the wall (*Epstein* 1994; *Lüttge et al*. 2002; *Currie & Perry* 2009; *He et al*. 2013).

Formation of silica deposits

After it has been deposited in accumulative plants, silicon occurs in the form of amorphous silica hydrate (opal phytolith). There appears to be a positive correlation between transpiration, metabolic activity (photosynthesis) and silica accumulation. But in old examples of certain species the deposits take place in the chlorenchyme (tissues containing chloroplasts), thereby reducing gaseous exchange and consequently the performance of photosynthesis (bamboo) (*Bauer et al.* 2011).

The process of silification happens in two principal stages. First of all, while the cell is still active, silicic acid accumulates in the primary wall (cf. above). The synthesis of the secondary wall initiates the process of programmed cell death, leading to the second stage of silification, i.e. the massive accumulation of supplementary silicic acid and its polymerisation into silica. Silica is deposited in the cells after the breakdown of the protoplasm, and increasingly so at the end of the cycle (*Strüh* 1989; *Gehlig* 1994; Hodson & Sangster, cited by *Cooke & Leishman* 2011; *Bauer et al.* 2011; *Law & Exley* 2011) in damaged or old cells. Silica deposition is intimately associated with cellulose and appears as a process analogous to lignification.

Specific locations are dedicated to silica uptake whereas adjacent cells cannot do it and can actively reject it. Silica is primarily deposited at the periphery in cell walls, in the epidermis and cells of sheaths around sap-transporting vascular bundles, but also in extra- and intracellular spaces, for example in the form of an extracellular layer between the epidermis and the cuticle. All organs are involved: root, stem, leaves, trichomes, sheaths of transport vessels and reproductive organs. When the *Si* content increases, other deposits (commonly called 'silica bodies') form in the interior of particular cells dispersed in the plant parenchyma. Silica deposition is irreversible. Once deposited, silica can no longer be used (*Epstein* 1994; *Ma et al.* 2001; *Bauer et al.* 2011).

Trichomes are the favoured locations for the deposition of silica. The term 'trichome' commonly refers to a set of bristles or a coat of hair. This definition is extended to comprise any excrescence on the epidermal surface such as papillae and scales (*Brice* 2011). A well known example is this of cotton fibres where silica plays a part in their development. In the case of cucumber (*Cucumis sativus*, Cucurbitaceae), the trichomes comprise a fine white powder on the surface of the fruit. It has been shown that the presence of trichomes results from the absorption of silicon by the transporters. A mutation renders them incapable of absorption and the cucumbers are thereby without trichomes (*Epstein* 1994; *Mitani et al.* 2011).

The surfaces of spores and elaters of horsetails (*Equisetum arvense*, Equisetaceae) are covered with small particles containing proteins and polysaccharides. These particles are protected by a coating of silica. At the moment of germination, the particles coated with silica are destroyed and provide substances useful to the developing young seedling, such as arginine and *Si*, both of which are known to be essential to its growth. Furthermore, large amounts of silica have been detected at the tip of the spore's germ tube during development, where it probably plays a part in reinforcing and supporting tissues while the tube digs its way into the soil (*Currie & Perry* 2009; *Law & Exley* 2011).

As a mineral silica has a determined shape, while silica phytoliths have a very large variety of forms, both in morphology and size. Their formation is a function of species and genotype and it is influenced by environmental conditions. This indicates the part played by extrinsic factors, notably those of an organic matrix where the deposits form. Among the constituents of this matrix, researchers have identified proteinaceous compounds of a structure related to that of collagen and certain sugar polymers (called polyolates) whose spatial configuration allows stable bonds with silicon of the type Si-O-C. Among the sugar polymers can be found *inter alia* cellulose, pectins, hemicelluloses (callose)[3] and xyloglycans (*Epstein* 1994; *Mann* 2001; *Currie & Perry* 2007; *Law & Exley* 2011; *Belton et al.* 2012).

Silicon and plant growth

The light effect of Si

The effects of *Si* on growth can be directly observed. At a high *Si* concentration in the culture medium (liquid), *Si* promotes the growth of cucumber, but this is not the case if the concentration is low. These effects are similar to those observed when exposing plants to intense sunlight: both result in increased root biomass and in increased photosynthesis efficiency (Adatia & Besford, cited by *Epstein* 1994). The same effects have been observed with rice. (*Ma et al.* 2001). These observations confirm the work of *Kolisko* (1953) who showed that adding finely ground silica to wheat culture medium, produced effects on development similar to those resulting from light exposure. Kolisko spoke of 'the light effect' of silica.

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[3] In horsetail (*Equisetum arvense*) it has been shown that the major sites of silica deposition are those where callose is also found. In vitro, callose accelerates (catalyses) the deposition of silica from a dilute solution (<2mM) of silicic acid. In the absence of callose no deposition of silica occurs. More callose is deposited in the oldest organs and the size of the silica deposits is a function of organ age (e.g. guard cells and those of the stomata ostioles) (*Law & Exley* 2011). It is the same with wheat (*Triticum aestivum*, *Poaceae*) where silica deposits occur in epidermal cells on the abaxial surface of the young plant's leaves, whereas in mature wheat the deposits are also on the adaxial surface. The walls of the sclerenchyma are the secondary sites of deposits around the transport vessels (*Epstein* 1994).

The efficiency of photosynthesis is characterised by the following: an increase in root biomass; leaves that are thicker, darker green and better positioned to capture the sun's light; a delay in leaf senescence; and a sharp increase in the amount of chlorophyll and RuBisCo (+50%; ribulose bis phosphate carboxylase oxygenase). RuBisCo is one of the most important enzymes of the living world, catalysing the first step in the Calvin cycle of photosynthesis (CO_2 fixation to the pre-existing carbon substrate ribulose bis phosphate). *Kolisko* (1953) adds to these criteria the shortening of the internodes and the smaller size of the first leaf.

Plant habit and leaf arrangement

The correlation between the abundance of silica and the mechanical robustness of a plant has been frequently observed. It results from silica incorporation into the cell wall, i.e. the deposits in the form of phytoliths (see above). Si, a crosslinking agent, improves the cell wall's mechanical properties and guaranties maintenance of the cellular shape. Plants grown in nutritive solutions or in open fields in which silicon has been supplied in sufficient quantities, resist lodging, do not collapse or bend and do not have a tendency to be laid flat. They maintain an upright habit and have a leaf arrangement that promotes light capture and a good functioning of photosynthesis, thus helping plant growth (Adatia & Besford, cited by *Epstein* 1994; *Kleiber et al.* 2015). Nitrogen fertilisation disrupts the arrangement of the leaves, especially if it is intense, leading to a decrease in light capture and growth. These effects are corrected by giving *Si* (*Ma et al.* 2001).

Si and carbon compounds

Si may be an alternative to cellulose and lignin, and its incorporation into the plant cell wall is economical from the point of view of energy consumption. Indeed, it has been estimated that the energy cost of its incorporation is tenfold lower than that of the incorporation of lignin or cellulose, carbon compounds produced by photosynthesis. *Si* is a material that is available in abundance allowing more economical use of carbon resources resulting from photosynthesis, and their diversion towards growth processes: carbon no longer has to do what silicon does (*Cooke & Leishmann* 2011).

Thus, *Si* contributes indirectly to increasing growth by allowing carbon to be used in the development of new leaves. Aquatic plants provide an interesting example. There is less light available for capture under water, and the output of photosynthesis there is weaker. Silica then assumes the structural (mechanical) role normally devolved to carbon compounds, and thus makes it possible to use them more efficiently in growth processes. This strategy of sparing carbon resources could likewise have been at work in the Miocene, characterised by a low atmospheric content of CO_2, where *Si* developed support structures (*Remer* 1996; *Cooke & Leishmann* 2011).

Short-lived leaves (cf. Poaceae), developed a growth promoting strategy thanks to silicon by optimising the use of carbon resources and nutrients. Photosynthetic output is at a maximum and relative growth is high. On the other hand, long-lived leaves (cf. dicotyledons, poorer in Si) prefer lignin to *Si* and have high construction costs, which they compensate for by a prolonged photosynthetic activity. The negative correlation between leaf longevity and their concentration of *Si* is commonplace in the plant kingdom. This is the case of annuals compared with perennials, as too with bushes and deciduous trees compared with evergreens.

In biotopes poor in available nutrients, leaves are long-lived, corresponding to a strategy allowing increased production from using nutrients and carbon resources. Furthermore, foliar longevity relies on the capacities for defence against herbivores. Long-lived leaves produce aversive substances such as tannins or large quantities of lignin. In contrast, short-lived leaves may get the same effect by accumulating silica.

Mitigation of nutritional imbalances

Adding *Si* to culture media may also mitigate nutritional imbalances and thereby improve growth. This has been observed when the concentration of phosphorus and zinc in the culture medium of cucumber is out of balance. The effect obtained is the same as by correcting the concentrations of zinc and phosphorus in the medium (*Epstein* 1994). *Si* given in sufficient amounts optimises the internal use of phosphorus in rice cultivated on deficient soils. Inversely, an excessive tissue content of phosphorus has a negative effect on growth through the inactivation of zinc, a major element in plant growth, by inhibiting enzyme activity and generating an abnormal intracellular osmotic pressure. Giving *Si* reduces the absorption of phosphorus and corrects the harmful effects (*Ma et al.* 2001, 2011).

Si may also modify nutrient absorption from the medium even if its composition is satisfactory (*Kleiber et al.* 2015). Thus, *Si* influences the absorption of nutrients such as iron, zinc, potassium and phosphorus (*Ma et al.* 2001). In the case of rice, growth increases with the addition of *Si* (1.66 mM). The effect observed is correlated with the reduction in the calcium content of the leaves. The foregoing observation is confirmed by other findings with non-accumulative plants such as lucerne (*Medicago sativa*, Fabaceae) and canola (*Brassica napus* L., Brassicaceae), as well as with accumulative plants such as common phragmites (*Phragmites australis*, Poaceae), cotton (*Gossypium hirsutum L.*, Malvaceae) and wheat. Silicon reduces calcium absorption by reinforcing the Casparian strip with deposits of silica, lignin or suberin (Ma & Takashi, cited by *Epstein* 1994; *Mehrabanjoubani et al.* 2015). These observations accord with those of Steiner (1923, 1924) according to which the effects of *Si* and lime are antagonistic.

Other effects of Si on development

The positive effects of *Si* added in large amounts to culture media may relate to specific aspects of plant development without there being any observable effects on growth. For example, they may relate to the reproductive yield which translates into an increase in the number of viable seeds. Thus, in rye brome (*Bromus secalinus*, Poaceae), the late root shoots, stems, leaves and inflorescences develop in the same way regardless of the silicon concentration of the nutrient medium, but the reproductive yield is enhanced in the presence of large quantities of silicon. It is the same in wheat (*Triticum aestivum*, Poaceae) where the grain yields are greater when the ears are more silicified (Hodson & Sangster, cited by *Epstein* 1994).

The positive effect of *Si* on growth may perhaps be demonstrated indirectly by experiments on mitigating toxic effects. Thus, manganese, an oligoelement, becomes toxic at high concentrations. In such conditions, barley grows poorly. But when *Si* is added to the medium, growth is significantly improved, root and shoot biomass is approximately doubled compared with plants grown in its absence (*Epstein* 1994; *Kleiber et al.* 2015).

Si as a soil improver

The role of *Si* has been tested in open fields with major cultural plants such as rice (*Oriza sativa*, Poaceae) and sugarcane (*Saccharum* sp., Poaceae) on very specific soils such as histosols in the Everglades (peaty soils rich in partly decomposed organic matter) and ultisols (leached soils of tropical rainforests, poor and infertile, containing little silicon). The results showed that improvement with silicates increased the silicon content of plants (sugarcane, rice, barley) and the yield in the proportions between 50 and 100%. It is for this reason that fertilisation with silicates has become common practice in such cultures (*Epstein* 1994).

Silica and stress reduction

Si in plants triggers a wide range of natural defences that help reduce the effects of abiotic stress, heavy metal toxicity, drought, water excess, wind, extreme temperatures, salinity, nutritional imbalance and the effects of biotic stress due to nematodes, fungi, bacteria, viruses, insects and other herbivores. Abiotic stress affects the whole plant, or at least all the root system and stem, whereas biotic stress is a localised attack. Admittedly, in the latter case, and contrary to abiotic stress, mechanisms of signal transmission over long distances play an important part. In accumulative plants, these effects are correlated with silica deposition in tissues, a large accumulation appearing to be necessary (*Epstein* 1994, 2009; *Ma et al.* 2001; *Richmond & Sussman* 2003; *Currie & Perry* 2007; *Liang et al.* 2007; *Yamaji et al.* 2008; *Cooke & Leishman*, 2011; *Ma et al.* 2011; *Mitani et al.* 2011).

Reduction in toxicity of heavy metals and toxic metalloids

At present, soil pollution by heavy metals is becoming a concern. Addition of *Si* to culture media reduces toxicity according to complex internal and external mechanisms, and improves plant growth. Toxicity reduction could result from reduced root absorption, co-precipitation with *Si* in the cell wall or cytoplasm, or a more homogeneous distribution in the leaf parenchyma. The insolubilisation of toxic minerals leads to a significant reduction of their absorption, their transport in tissues and their interference in biochemical reactions. To that is added the reduction of membrane peroxidation by increased production of enzymatic and chemical antioxidants. External mechanisms reduce root absorption resulting from the formation of insoluble *Si*-metal complexes (case of aluminium-Al^{3+}) or complexes with phenol derivatives released in large quantities under the influence of *Si* (*Epstein* 1994; *Liang et al.* 2007; *Ma et al.* 2001, 2011; *Ali et al.* 2013; *He et al.* 2014; *Kleiber et al.* 2015).

Silicon and toxicity of metals and metalloids: some examples

The reduction in metal toxicity by *Si* has been studied in many plants with different metals. The toxicity of manganese and its correction by *Si* has largely been studied in barley (*Hordeum vulgare*, Poaceae), bean (*Phaseolus vulgaris*, Fabaceae), cucumber (*Cucumis sativus*, Cucurbitaceae), tomato (*Solanum lycopersicum*, Solanaceae; *Kleiber et al.* 2015). It is the same with the toxicity of other elements, among which chromium, aluminium and cadmium have been studied in barley (*Ali et al.* 2013), sorghum (*Sorghum bicolor*, Poaceae), soya (*Glycine max*, Fabaceae), tomato (*Solanum lycopersicum*, Solanaceae), white spruce (*Picea glauca*, Pinaceae), rice and maize (*Zea mays*, Poaceae).

The bladder campion (*Silene vulgaris* subsp. *humilis*, Caryophyllaceae) is very tolerant of heavy metals. The effects of toxic metals (Zn and Sn) are neutralised by the mechanisms described above. *In Arabidopsis thaliana* (Brassicaceae) co-precipitation of silica and zinc has been observed in cytoplasmic vacuoles of mesophyll cells and in the nucleus.

In the form of arsenates or arsenites, soil arsenic (due to vulcanism, mining industry, coal-fired power plants and certain pesticides) prevents germination of seeds and elongation of stems in tomato. The toxic effect is a function of the genetic structure of the tomato variety. Adding silicate to the culture medium reduces this toxicity (*Marmiroli et al.* 2014).

Si and salinity

This principally concerns the salinity due to sodium salts at high concentrations. Salinity seriously damages plasma and vacuole membranes as well as those of chloroplasts. The effect of *Si* is on correcting membrane damage by reducing its permeability, inhibiting lipid peroxidation, reducing tissue concentration of sodium, increasing that of potassium and calcium and storing sodium in vacuoles. It follows the reduction in osmotic stress and the increase in root absorption of water as well as the efficiency of its use (reduction in evapotranspiration). Trophic functions are stimulated overall: root activity, photosynthetic yield improvement (increased CO_2 supply) and significantly increased biomass. *Si*'s correction of the negative effects of salinity has been observed in rice, wheat, barley, cucumber, tomato and even in *Prosopis juliflora* (Mimosoideae) (*Ma et al.* 2001, 2011; *Habibi et al.* 2014).

Si and drought

Drought impedes growth, reduces stem elongation, reduces limb expansion and stoma movements, increases reactive oxygen species (ROS) which damage membrane lipids (plasma, vacuole, chloroplast) and photosynthesis proteins. Giving *Si* corrects these negative effects by modifying the same physiological and biochemical activities as in the case of excessive salinity. It should be noted that the effects of *Si* are only explicit in case of drought: significant differences are not observable between plants with or without a *Si* supply if sufficient water is available. (*Gong et al.* 2005; *Hattori et al.* 2005; *Ma et al.* 2001, 2011; *Katz et al.* 2013; *Habibi & Hajiboland* 2013; *Shi et al.* 2014; *Cao et al.* 2015). The formation of a sub-cuticular layer of precipitated silica is another means contributing to the reduction of drought effects by reducing evaporation (*Ma et al.* 2001; *Bauer et al.* 2011).

Si and herbivores

There are many ways that plants defend themselves against herbivores (mammalian, foliar insects, suckers and piercers) including thorns, prickles, trichomes, raphides and hardness of epidermal cells. *Si* takes part in these physical defence mechanisms. Deposits of silica, the hardest material in plant tissues, form a barrier that reinforces the ruggedness of leaves and stems, reducing their acceptability and digestibility thus preventing, reducing or delaying attack by herbivores. Furthermore, silica deposits interfere with the biological functions of herbivorous insects, delay egg laying, increase larval and nymph mortality, and inhibit their efficient use of nitrogen. As a result, herbivorous insects are exposed for a longer time to their natural predators.

The efficiency of this barrier is dependent on the density and uniformity of the silica deposits. It is an alternative in systems that bring into play carbon derivatives (cf. phenols). Silica accumulation may be induced and stimulated by the damage caused by herbivores, which constitutes a useful strategy if the herbivory is intermittent or predictable. Thus, the foliar concentration of silica in *Lolium perenne* and *Festuca ovina* (Poaceae) increases by 400% after repeated herbivore intervention (sheep) (*Hunt et al.* 2008; *Bauer et al.* 2011; *He et al.* 2014).

It has been established that *Si* in the form of silicic acid induces the biosynthesis of systemic or specific defence substances of a given biological agent. Its effect is more clearly detectable after the activity of a predator (eliciter). A cascade of biochemical events follow (induction of signals and biochemical mediators) and lead to the production of specific proteins which, at the nucleus level, repress or activate specific genes for the synthesis of defence substances. Only silicic acid is effective, acting after being linked to a cellular organic compound to form a complex which triggers the sequence of events described above. On the other hand, silica (opal phytolith) is completely inactive (*Reynolds* 2009).

These biochemical mechanisms lead to the synthesis of defensive enzymes and volatile substances among which are phytohormones such as salicylic acid, ethylene and jasmonic acid. Jasmonate and methyl jasmonate, its volatile form, plays a crucial part in defence against herbivores (*Augereau* 2008; *Reynolds & Keeping* 2009; *Ye et al.* 2013). Overall, *Si* reinforces the effects of jasmonate and increases its concentration and the synthesis of the different substances that it initiates – e.g. digestive enzyme inhibitors, trypsin inhibitors, Bowman-Birk inhibitor, i.e. compounds that interfere with herbivore digestion. Their effects on insects may be those of appetite suppressants. Furthermore, jasmonate increases silica absorption and, correspondingly, its accumulation in or on the epidermis. The effects of *Si* are modulated by jasmonate and, reciprocally, the effects of jasmonate are amplified by silicon. The interaction between *Si* and jasmonate probably constitutes a widespread mechanism whereby *Si* increases the resistance of plants against biotic attack.

Si and plant disease

Si is essential for ensuring resistance to parasites (viruses, bacteria and fungi). For example, *Si* added to the culture medium makes cucumber resistant to powdery mildew (*Spherotheca fuliginea*). It is noteworthy that even after repeated fungicide application, the fungal disease appears on plants cultivated without *Si* and not on plants treated with *Si*. The same method succeeds for vines. This observation is particularly interesting as it seems more effective to add *Si* to the culture medium rather than treating with fungicides (*Epstein* 1994).

The results are of the same order with rice and other cereals. For example, when rice is cultivated in soils supplemented with *Si*, a clear increase in yield is seen and a dramatic reduction in the severity of fungal disease (pyriculariosis, foliar wilting, brown spot, leaf scald, stem rot and mildew). The response may vary according to the rice genotype studied. Overall, the results obtained are impressive and economically valuable (*Yamaji et al.* 2008).

Ma et al. (2001) showed that nitrogen fertilisation increases pyriculariosis in rice, more so with increasing nitrogen content. Adding *Si* increases the Si/N ratio in tissues and significantly reduces the effect of nitrogen in promoting rice pyriculariosis (*Ma et al.* 2001).

The observations are the same with non-accumulative plants, e.g. tobacco (*Nicotiana tabacum*, Solanaceae). *Si* protects, retards or reduces the lesions caused by ring spot virus, and the content of *Si* in leaves is influenced by the virus: the leaves of infested plants contain four times the amount of *Si* compared with when infection is absent. On the other hand, *Si* gives no protection against tobacco mosaic virus, and in this case the content of *Si* depends only on the *Si* available in the medium (*Zellner et al.* 2011).

Moreover, no clear effect is observed of supplemental *Si* on the implantation of holoparasites of the genus *Striga* (Orobanchaceae) on rice, sorghum, millet (*Milium sinensis*, Poaceae), maize, corn and sugar cane (*Epstein* 1994).

Discussion and conclusion

Essential character of Si

Si is present everywhere and because of this it constitutes a ubiquitous laboratory contaminant. For this reason, it is difficult to prepare a medium that is deficient in *Si* so as to be able to demonstrate its essential character with plants, apart from the Equisetaceae (Chen & Lewin, cited by *Epstein* 1994; *Law & Exley* 2011). When *Si* is available to plants it obviously plays an important part in their mineral nutrition, growth, mechanical robustness, and resistance to hostile conditions in the surroundings including herbivores and diseases. That is why *Epstein* (1994) considered *Si* as a 'quasi essential' element for plant development. Plants grown in nutrient solutions containing *Si* only as an environmental contaminant are considered abnormal and are, in a certain way, experimental artefacts (*Rafi et al.* 1997; *Epstein* 2009; *Cooke & Leishman* 2011). Since Epstein's work, it has been shown that *Si* assures the viability of cells in culture (callus cells of rice) and ensures the stability of their shape during the stages of mitosis (cell division). In its absence, cells in culture die and are incapable of completing mitosis. Small quantities of *Si* are sufficient for maintaining cell shape and its mechanical properties. Although certain plants appear to exclude *Si* it is clear that for many plants, *Si* is a beneficial element (*Epstein* 2009; *Ma et al*. 2001; *Ma et al*. 2011), even a crucial element (*Liang et al*. 2007; *He et al*. 2013). This beneficial characteristic often expresses itself more clearly in the case of stress. To summarise, one could say that *Si* preserves the expression of the essential nature of the plant.

Physiological roles of Si

It is now evident that the physiological role of *Si* cannot be confined to physical and mechanical properties of deposits, and that research can no longer focus on accumulative plants because all plants studied contain it (*Hodson et al*. 2005). *Si* may be an important factor in the function of their leaves, but this ignores many siliceous phenomena in non-accumulative plants and of plants in wild ecosystems (*Katz* 2014).

Silica is a crosslinking agent of the cell wall constituents reinforcing the cell periphery and contributing to the robustness of the plant. It acts alone (monocotyledons and primitive plants) or in association with boron (dicotyledons). In accumulative plants it is deposited at the periphery in specialised tissues. These deposits constitute support structures that reinforce the robustness and firmness of stems, and which can at the same time improve the carbon balance by substituting for lignin or other carbon compounds. In some ways, the formation of these true exoskeletons is reminiscent of bone. But biogenic silica (phytoliths) constitute definite non-mobilisable deposits. They increase with tissue age indicating the senescence or even the withering of the plant. It is exactly the opposite with the human being where the silica content of structural tissues is greatest at birth and decreases with age, its deficiency being correlated with degenerative diseases and sclerosis (*Gehlig* 1994; *Girke* 2012; *Hibou* 2019).

One of *Si's* essential functions involves defence phenomena. It acts as a modulator of tolerance of plants to abiotic and biotic stress, by deploying physical and biochemical means. The fight against herbivores is possible thanks to the silica deposits, but also to the activation of complex biochemical processes that lead to the repression or activation of genes and the synthesis of corresponding effectors. The synergistic interaction between silicic acid and jasmonate, whose production induces that of a variety of defence substances, is an example of the diversity of *Si* effects in defence processes.

The interference of *Si* in calcium absorption, which it reduces, stimulates growth. Furthermore, *Si* corrects the poor positioning of leaves for light capture caused by excessive nitrogen fertiliser (Ma & Takashi, cited by *Epstein* 1994; *Ma* 2001). This observation is interesting because calcium and nitrogen both support the astral (*Steiner* 1923, 1924).

The light effect of soil silica

Steiner's indications (1923, 1924) formed the basis of the work of *Kolisko* (1953) who was the first to show experimentally the light effect of *Si* on plant development. Steiner's views put the role of *Si* in a very much wider context, both cosmic and telluric. According to his works, soil silica and deeper layers of the Earth's crust behave as a light sensor, and because of this become similar to a sense organ for the whole Earth. The silica of rocks, soil, water, air and heat generates an environment that is favourable to the growth of plants. During their growth, this 'silica environment' transmits to them, via the root system and the cambium, the activity of formative forces of the fixed stars and the superior planets Mars, Jupiter and Saturn, for the creation of structures and substances. During growth phenomena, this activity radiates from below upwards, from the roots to the seeds, from the moist darkness of the mineral world towards the surrounding cosmos. Silica acts as a formative principle in close association with carbon to give structure to the plant from its roots or from its branches to its shoots and inflorescences. Silica also acts in the realm of substances (metabolic) and gives rise to colours (red and the influence of Mars, white, yellow and the influence of Jupiter as well as blue and the influence of Saturn), and to fragrances, nectar, sugars and complex substances (starch, proteins and oils). In doing so it gives plants nutritional properties of interest to animals and humans (*Steiner* 1924).

The formative forces transmitted by silica from the soil to the root act in an enlivening manner and make the root the organ where a large vital potential is concentrated (buds, root apices, storage substances). Its formative influence is expressed by whole roots, unbranched or tap roots, contrary to roots influenced by 'lime' which are markedly branched. The radiant characteristic of 'silicic acid' also finds its expression in the peripheral distribution of trichomes on the parts of the plant exposed to the light. They can be rich in silica and constitute the sites of deposition of essential oils.

The phenomena described are largely confirmed in practice in biodynamic agriculture where silica plays a leading part in plant health and in the foods that plants produce (see box, *Masson* 2016). They must be extended through the study of the influences of 'lime' and 'clay' based on academic knowledge and the findings of anthroposophy.

Effects of silica in agriculture

(*Masson* 2009, 2016)

In his agriculture course Steiner (1924) discussed the role of silica in the living world. He indicated that silica mediates solar forces modified by the superior planets Mars, Jupiter and Saturn and by the fixed stars. These forces once transmitted to plants allow them to express their shape and produce substances. Steiner described the different forms of useable silica:

- quartz (horn silica or preparation 501), feldspar, orthoclase
- silica accumulative plants such as horsetail (*Equisetum arvense*, Equisetaceae)
- parts of plants and whole plants that are non-accumulative in which forces conveying those of silica are at work (silicic acid process), like dandelion flowers (preparation 506). This preparation influences the absorption of silicic acid by plants and renders it more sensitive and capable of attracting to itself useful substances and forces present in the distant surroundings
- clay, another form of mineral silica (hydrated aluminosilicate).

Today various siliceous mineral products are used in agriculture, such as powdered granite and basalt, diatomaceous earth (Kieselgur) and radiolaria; clay is used in dusting or as a spray suspended in water.

Remer (1996) described Si as 'the forgotten element of modern agriculture'. Nowadays, research on silica is on the increase, and is beginning to corroborate field observations made by practitioners of biodynamic agriculture (see above).

The action of preparation 501 on vegetation varies according to: the nature of the soil, whether siliceous or calcareous; the warmth of the climate; dryness or wetness; the season (spring, summer or autumn); the time of day (morning, evening) and frequency of application; the physiological stage of the plant (before flowering, before or after harvesting); and its state of 'fatigue' or health (incidence of viruses).

Horn silica acts through its light effect and influences food quality

The relationship between silica and light has been demonstrated by *Kolisko* (1953) and other authors such as *Klett* (1968), Adatia & Besford (1986, cited by *Epstein* 1994) and *Ma* (2001). Klett showed that cereals grown in the shade and treated with powdered horn silica behaved in a way comparable to growing them exposed to the sun. When the plot is shaded and without silica, substance formation and maturation are disturbed.

With vines, the effect of diluted and dynamised horn silica (preparation 501) depends on the plant's vigour and phenophase. It moderates the excessive vigour of luxuriant vines, supports or even stops the growth of somewhat weak vines, limits the formation of secondary lateral branches when sprayed together with a valerian preparation (preparation 507) just before flowering and at the stage of fruit set (*Masson* 2015). Vine leaves treated with horn silica sprays are glossier and their orientation improves light capture. Horn silica improves phenolic maturity of grapes and at the same time increases sugar content (approximately 10% more) (*Masson* 2009; *Meissner* 2015). The resulting vines are more aromatic, richer in polyphenols and the distribution of acids is more balanced.

In arboriculture, the light effect of horn silica improves fruit colour, even in the interior of tree crowns, in shady locations where sunlight weakly penetrates. For trees and vines, horn silica promotes the transport of reserves in trunks and roots. This allows a more regular bud break in the following spring.

In horticulture, with vegetables that form roots as winter storage (carrot, parsnip, beetroot, black radish, potato etc.) spraying horn silica in the evening some weeks before harvest helps foliage withering and the accumulation of sugars and aromas in the underground parts.

Generally horn silica increases product quality and improves storage properties (spinach, potatoes and cereals; *Spiess* 1994) and resistance to weevils during storage as well as reducing Fusarium toxin production in cereals (*Berner et al.* 2005).

Other effects: silica reinforces and regulates the expression of the plant's identity

With vines, spraying horn silica increases shoot length and improves 'verticalisation' (increase in the angle of the shoot in relation to horizontal). Furthermore, it reduces the number and length of secondary lateral branches and of secondary fruit bunches, improves wind resistance and shoot flexibility, which helps with trellising. Disease resistance increases, notably to mildew and botrytis (grey rot, cf. *van der Meer et al.* 2009).

Glossary

(*Brice* 2011)

abiotic: abiotic stress is a physical or chemical influence harmful to plants

Casparian strip: thickenings formed in the transverse and radial walls of endoderm cells (roots), above all composed of suberin, a complex of long-chain fatty-acids and alcohols with hydrophobic properties.

biotic: biotic stress is a harmful influence on plants due to living organisms such as viruses, bacteria, fungi, herbivores etc.

biogenic crystals: crystalline mineral forms produced by a living organism in its tissues, e.g. bone, eggshell, sea urchin spicules and renal calculi.

exoskeleton: supportive structure formed at the periphery of an organism, e.g. oyster shell.

holoparasite: plant incapable of photosynthesis attached usually by its roots to a host plant in order to draw out carbon substances necessary for its growth, e.g. orobanche (broomrape).

lignin: polyphenol compound comprising an assemblage of monomers of three phenyl-propane alcohols (coumaric, ferulic and sinapic acids).

mesophyll: part of a leaf under the superior epidermis (adaxial) comprising palisade tissue and lacunar parenchyma.

phenophase: a particular stage in the development of a plant.

phytolith: biogenic crystal of silica.

spore: haploid reproductive cell (1n chromosomes) resulting from meiosis (chromatin reduction) and developing in a gametophyte (tissue producing gametes).

stoma: hole in the aerial surface of a plant intended for gaseous exchange (O_2, CO_2, H_2O).

trophic (function): that relates to the nutrition of living tissue.

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