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Review

Phytoliths – From the Formation of Biominerals to the Risks of Oxalate Ingestion in Plants – Mini Review Part I

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The presented mini review examines phytoliths in plants and microorganisms, focusing on their formation, physico-chemical properties, content in plant, and effects on livestock and human health. Phytoliths are primarily inorganic solid materials – biominerals, often formed by organic acids within plant tissues. They are relatively insoluble, enduring diverse environmental conditions (pH 3–9). Phytolith content in plant tissue varies significantly – from 2.5% to 70% – influenced by plant species, fertilizer use, climate, and agronomic practices. Two main types, oxalates, and silicon dioxides in opal form, are most commonly studied. Oxalates, found in both animal and human diets, can bind essential cations like calcium and magnesium, reducing their bioavailability and potentially increasing toxicity risks. When ingested, these oxalates may form insoluble compounds linked to physiological effects leading to risks associated with kidney failure. Phytolith research is interdisciplinary, spanning fields like archaeology, medicine, agriculture, nanotechnology, ecology, and environmental science. The Part I of this mini review explores the basic principles of the biomineral formation and their diversity. It goes into more detail about oxalates, their typical properties and occurrence in plants with risks for human and animal health after ingestion. The Part II of the mini review will discuss phytolith classifications, their utility, and factors influencing the formation of the second most common phytoliths made of silicon dioxide.

Keywords: phytoliths, oxalates, plants, human and animal risks

1 Introduction

In the past decade, there has been increased emphasis on human and animal nutrition, as diet directly influences growth, development, and health. However, academic literature contains little emphasis on insights into phytoliths, from "phyto" meaning plant and "lithos" meaning rock, which could affect various physiological functions. Many plants, including animal fodder and human food, contain oxalates, with levels ranging from 3% to 70% (Nakata, 2003).

High content of oxalates in the diet could lead to urinary, gallbladder, and kidney stones. Approximately 75% of all kidney stones are primarily composed of calcium oxalate (Massey, 2003, Chaudhary et al., 2010). The remaining oxalate concentrations in urine are a risk factor for stone formation in vegans (Massey 2003, Beghalia et al., 2008), with the greater risk associated with raw vegans. Also, phytoliths reduce the absorption of iron and calcium, potentially leading to hypocalcemia, a condition characterized by low calcium levels in the blood (Waldmann et al., 2004). Current knowledge suggests that stone formation could be prevented by limiting foods rich in oxalates. In Europe, the typical diet has relative lower oxalate content, which reduces the risk of associated health

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issues, however, the situation may change over the long term (Siener et al., 2020).

The biominerals formation, or biologically induced crystallization of solid inorganic parts, is related to term "soil mineralization". The process that transforms organic matter into simpler compounds, primarily water, carbon dioxide, sulphur dioxide, and ammonium hydroxide, releasing nutrients (such as calcium, sodium, and potassium) bound to organic compounds associated with releasing energy (Čurlík & Kolesár, 2014). In Anglo-Saxon literature, the term "mineral" is defined as a crystalline phase which is equivalent to solid substrates, precipitates, and similar entities. It is characterized by a specific stoichiometry and crystalline structure (Mann, 2001). In the context of human nutrition, the term "mineral" is often defined as a nutrient or chemical elements most commonly in soluble ionic species that an organism requires to perform certain vital functions (Kaushal et al., 2022).

Therefore, the aim of this study is to examine phytoliths formation in plants, which have both direct and indirect impact on the nutrition in terms of food consumption. Additionally, understanding their significance is increasingly relevant in agronomy, veterinary and medical science.

2 Formation of Biominerals – Phytoliths in Various Species of Micro/organisms

Biomineralization must be understood in the context of Earth's evolutionary history, where it serves primarily as a protective function, forming exoskeletons in microorganisms. Biological mineralization began around 3.5 billion years ago, evident in stromatolite formations (Mann, 2001). About half a billion years ago, life proliferated, forming various shells and microskeletons composed of minerals such as calcium carbonate, calcium phosphate, and silica, among others that occurred primarily in marine environment (Rashid et al., 2019). Evolutionarily, biominerals serve as a reservoir of ions for various cellular functions, enabling movement and environmental sensitivity to gravity and the magnetic field. Iron-containing biominerals, such as nanoparticulate formed by magnetotactic bacteria (Strbak et al., 2022), have currently particular significance for their biomedical potential.

The process of biomineralization involves elements such as Ba, Ca, Cu, Fe, K, Mg, and others, which form a solid precipitate from the ambient environment (Ma et al., 2021). It differs from classical geological crystallization, as microorganisms partially regulate the biomineral formation through enzymatic (metabolic) processes based on their genetic information – a feature highly attractive to biomimicry and biomimetics (Ma et al., 2021). This mechanism is based on the atom-by-atom principle, also known as "self-assembly," which poses the state of the art for future industrial applications including bio-nanotechnology (Grzelczak et al., 2010, Kolenčík et al., 2014).

These minerals are not completely equivalent to the ones formed by natural inorganic processes because the organisms influence the initial conditions and the whole process of formation (Crowther, 2009, Addadi & Weiner, 2014). In terms of diversity, direct or indirect biomineral production has been described in bacteria (Strbak et al., 2022), fungi (Šebesta et al., 2022) or plants (Kolenčík et al., 2014). Among animals, biomineralization was observed e.g. in cnidarians, mollusks, and arthropods (Addadi & Weiner, 2014).

According to Mann (2001), biomineralization occurs in two ways:

1. biologically induced mineralization, where biominerals form as secondary (often toxic) products of the organism without many useful functions, such as urinary and gallstones, and other organominerals with chemical nature based on calcium and magnesium carbonate, and manganese and iron oxides;
2. biologically controlled mineralization, which are primary metabolic products with specific roles such as shells, exoskeletons, and bones.

This group can be divided into:

a) extracellular formation, where ions are transported out of the cell, producing extracellular organic matter (matrix) from proteins and polysaccharides, leading to the formation of bones and teeth;
b) intercellular, where minerals are produced in intercellular spaces, producing a different kind of exoskeleton, especially in unicellular organisms living in communities;
c) intracellular excretion, where minerals are formed inside the cell in vacuoles and are later transported out to the environment.

3 Formation of Phytoliths in Plants and Evaluation their Advantages

The synthesis of phytoliths – oxalates is a part of the plants' natural metabolism involving several biochemical pathways, for instance, from oxaloacetate as an intermediate in the tricarboxylic acid (TCA) cycle or through enzymatic decarboxylation. Also, they could form in light-exposed leaves from glyoxylate through photorespiration, the glyoxylate cycle, or ascorbic acid breakdown (Kaushal et al., 2022; Li et al., 2022).

Phytoliths are naturally integrated in plants tissues, and after their decay, they become part of the soil environment. On average, 1 gram of dry phytomass contains 2 to 20 mg of phytoliths, though this varies by plant species (Sharma et al., 2019). The size typically ranges from 5 to 200 µm, with a characteristic morphology and irregular surfaces that could be variably coloured or colourless (Mann, 2001, Crutcher & Crutcher, 2019). They are relatively stable in a wide range of acido-basic soil conditions (pH = 3–9) and are well preserved in high humidity or dry conditions. They occur in most environments, such as rainforests (Crifò & Strömberg, 2020), mountain ecosystems (An et al., 2015), or others. Due to their relative stability and characteristic properties, they serve as a suitable diagnostic tool in various scientific disciplines. In palaeontology, archaeobotany and paleoecology, they are widely applied to the reconstruction of vegetation dynamics and life cycle of micro/organisms or their ambient conditions (Chen, 2024), indicate climate changes (Rahman & Kawamura, 2011), or determine ^{14}C isotopes, e.g. for medical purposes (Park & Gregory, 1980). When they are affected by high temperatures, their morphology changes, at 500 °C, no changes are visualized; at 600 °C, minor changes are noticeable; at 700 °C, more significant morphological modifications are shownand at 800 °C, the phytoliths completely melt and transform (Wu et al., 2012).

Phytoliths can have many modifications (Crutcher & Crutcher, 2019) which bind various secondary or trace elements. Additionally, they may contain small amounts of alkali metals, alkaline earth metals, metalloids, nonmetals, transition metals, lanthanides, and actinides (Hart, 2001). During the uptake, storage, and sedimentation of silica in cells, these accompanying elements are gradually incorporated into the phytolith. As noted by Hart (2001), phytoliths from the leaves of two plant species, *Actinotus helanthi* and *Triodia mitchelli*, growing in the same sediment, contained these accompanying elements in different quantities. Different types of phytoliths in various parts of plants, in the calcium oxalates form (Figure 1 a, b, d) and opal from of silica dioxide, are shown in (Figure 1c).

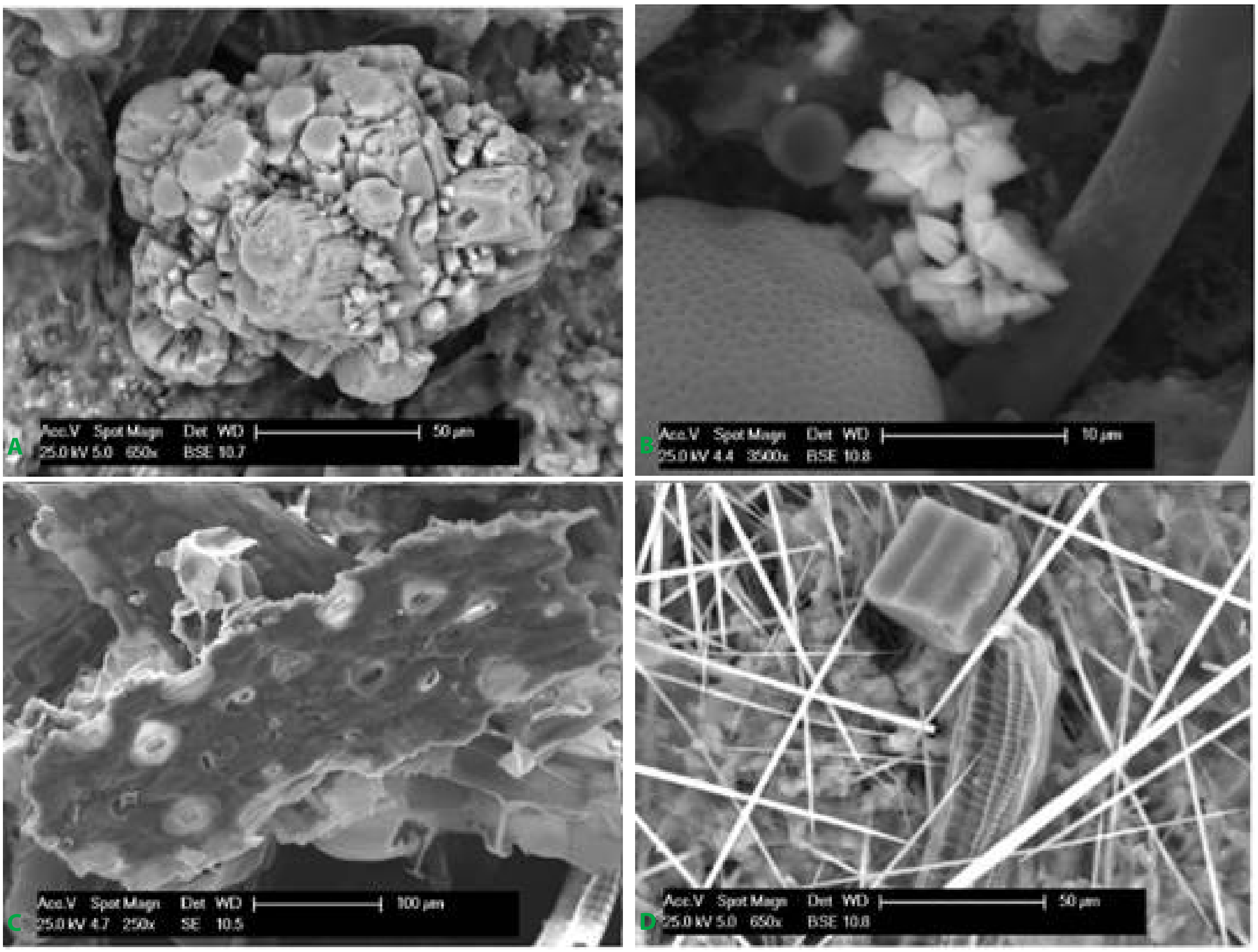

Figure 1 The images depict various types of phytoliths in different part of plants
A – stem of *Petroselinum crispum*; B – bract of *Tilia cordata*; C – spindle of *Zea mays;* D – leaf of *Aloe vera*, original image visualization was conducted using SEM (Scanning Electron Microscopy

4 Occurrence and Distribution of Soluble and Insoluble Oxalates

Oxalic acid (OA) and its thermodynamically stable crystalline forms, collectively referred to as oxalates, are generally recognized as insoluble compounds, predominantly calcium oxalate. This most commonly occurs in two crystalline forms including weddellite and whewellite (Figure 2a, b), that are present in all parts of plants across all plant kingdom species (Li et al., 2022), as well as in fungi (Šebesta et al., 2020) animals (Rahman et al., 2013), and humans (Massey, 2003).

OA primarily imparts an acidic taste to fruits and vegetables and commonly extends the post-harvest stability period (Hasan et al., 2023). In plants, oxalic acid plays various essential roles in functions including calcium regulation, and metal detoxification (Li et al., 2022). Oxalate poisoning could occur when animals consume large amounts of oxalate-rich plants, particularly those containing insoluble potassium oxalate (Young & James, 2019) where plant species such as *Oxalis* spp. offer highly acidic cell liquid with low pH (Rahman et al., 2013). In mammals, it is a metabolite of certain amino acids.

OA was first administered as a disinfectant in 1957 and is also used as a biological acaricide against mites in beehives or other functional bee life cycles. Since it is considered a natural compound found in honey, it is approved for application in organic beekeeping (Bozkus, 2023). Although OA is obtained through microbial production (Kumar et al., 2024), its properties make it useful as a disinfectant to eliminate bacteria and pathogens, a cleaning agent with potential in the food industry (Anang et al., 2006), and for wastewater purification, especially in controlling biofilm formation in distributed drinking water systems (Chu & Lu, 2004). OA is used in the production of oxalates, dextrin, cellulose, tartaric acid, purified methanol, glycerol, and stable hydrogen cyanide (Bastida et al., 2022; Koranian et al., 2022). Additionally, oxalate leaching enhances palygorskite's surface properties and ion release, making it a promising biomedical material for hemostasis (Yang et al., 2024).

Under laboratory conditions, oxalic acid appears as a colourless, odorless powder or granular solid with non-volatile and water-soluble character. Within a pH range of 5 to 9, it is distributed in solution as a soluble oxalate ion (Wiersma, 2011).

5 Content of Soluble and Insoluble Oxalates in Plants

In plants, oxalates occur as insoluble salts of calcium, magnesium, potassium, sodium, and other elements. Some plants contain much higher levels of oxalates and they are contained in grains, tubers, nuts, vegetables, and fruits (Lo et al., 2018).

Generally, the highest oxalate content is found in leaves, followed by seeds, with the lowest levels in stems. High oxalate concentrations are particularly found in tropical plants, where oxalates accumulate in reflection to drought stress and climate changes (Rahman & Kawamura, 2011). Examples of certain cultivated crops containing variable amounts of oxalate are shown in Table 1.

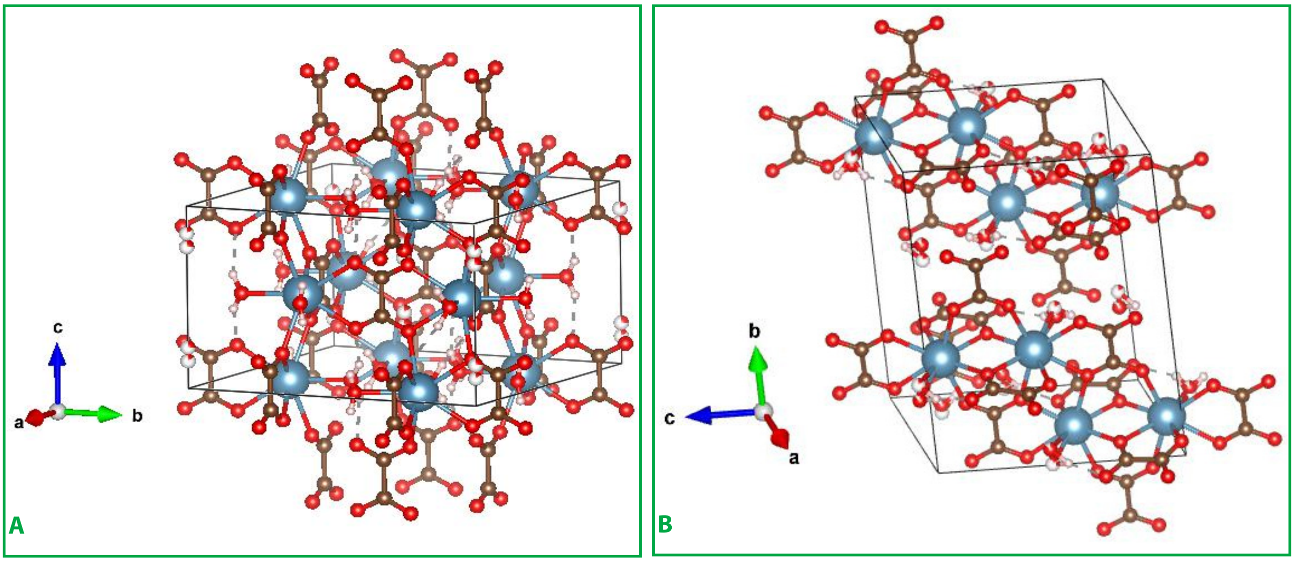

Figure 2 The atomic arrangement of calcium oxalates in its common forms
A – calcium oxalate dihydrate – weddellite $Ca(C_2O_4) \cdot (2.5\text{-}x)H_2O$; B – monohydrate – whewellite $Ca(C_2O_4) \cdot H_2O$, is shown using the Bohr model in VESTA program. In the model, calcium (Ca) corresponds to blue colour, carbon (C) is brown, oxygen is red, and H is visualized in pink one. The a, b, and c – axes pose the 3D vector geometry

Table 1 The content of soluble and insoluble oxalates in selected plants for consumption per 100 g

Plant species	Plant species	Oxalate content mg per 100 g
Garden parsley	*Petroselinum crispum*	1,700
Carrot	*Daucus carota*	500
Sweet potato	*Ipomoea batatas*	240
Radish	*Raphanus sativus*	480
Common bean	*Phaseolus vulgaris*	360
Cabbage	*Brassica oleracea*	35–190
Tomato	*Solanum lycopersicum*	50
Garlic	*Allium sativum*	360
Opium poppy	*Papaver somniferum*	1,620
Lettuce	*Lactuca sativa*	330
Celery	*Apium graveolens*	190
Halogetont	*Halogeton glomeratus*	120.8–300
African bristlegrass	*Setaria sphacelata*	10.2–60.9
Curly Dock	*Rumex crispus*	60.6–110.1
Sour Dock	*Rumex acetosa*	50.8–120.9
Three-Color Amaranth	*Amaranthus* gangeticus	80.6–110.9
Eatable Taro – Leaf	*Colocasia antiquorum*	70
Eatable Taro – Tuber		20.2
Common Beet – Leaf	*Beta vulgaris*	70.8–140.1
Common Beet – Tuber		6.8
Common Beet – Scabious		40–80.1
Spinach – Leaves	*Spinacia oleracea*	54–120.3
Spinach – Stem		15–41
Alfalfa – hey	*Medicago sativa*	9.6–11
Rice – straw	*Oryza sativa*	16–40
Common millet – hey	*Panicum miliaceum*	23
Soybean	*Glycine max*	67–350
White Goosefoot – leaves	*Chenopodium album*	93–185
Sowbane – leaves	*Chenopodium murale*	99–210

Source: Massey et al., 2001, Massey, 2003, Rahman & Kawamura, 2011, Čurlík & Kolesár, 2014, Lo et al., 2018, Crutcher & Crutcher, 2019, Siener et al., 2020, Li et al., 2022, Hasan et al., 2023

Animal feed crops with high oxalate content are widely cultivated in tropical and subtropical regions, such as *Halogeton glomeratus*, *Pennisetum clandestinum*, *Kochia scoparia*, *Cenchrus ciliaris*, *Pennisetum purpureum*, *Bassia hyssopifolia*, *Amaranthus* retroflexus (Rahman & Kawamura, 2011). Many studies indicate that the oxalate content in plants varies because of the genetic, climatic, and agronomic factors (Rahman & Kawamura, 2011).

6 Factors Influencing the Formation and Content of Oxalates in Plants

From a genetic perspective, it has been evidenced that different cultivars within the same region, subjected to identical agronomic practices and cultivation conditions, exhibited varying oxalate content (Massey, 2001). Regarding the oxalate's distribution within the plant, the highest concentration is found in the leaves, followed by the fruits and then the stems (Rahman et al., 2006). In the case of stems, there is also a notable correlation between their thickness, mechanical resistance, and higher oxalate content. Consequently, future academical and practical efforts should focus on selecting cultivars, breeding strategies, or forage varieties that accumulate lower oxalate levels in leaves, as ruminants exhibit a preference for consuming leaves over stems (Li et al., 2022).

Seasonal climate fluctuations significantly affect content of oxalate in some plants, where factors such as climate zones, precipitation, day length, and sunlight hours could alter oxalate content in plants that are potential forage. Also, soil moisture plays a role; for instance, Rahman and Kawamura (2011) reported that increased water uptake by *Atriplex halimus* could stimulate oxalate levels in its leaves. Similarly, Goyal & Kaur (2019) observed that high oxalate levels in *Pennisetum purpureum* hybrids during June and July reflect rapid accumulation during hot and rainy periods. Forages in tropical regions typically have higher oxalate levels than those in temperate zones, suggesting association temperature with oxalate plants accumulation (Rahman et al., 2006).

Since oxalate content could vary with the season and plant maturation, implementing appropriate agronomic harvesting practices is needed to prevent its excessive content. For instance, Abu-Zanat et al. (2003) observed higher oxalate levels in mature *Atriplex halimus* plants than younger seedlings. Analogically, Rahman et al. (2009) confirmed the same trend in *Pennisetum purpureum*, where oxalate content depended on the harvest interval. Strategies to reduce oxalate levels involving soaking, germination, cooking, or ensiling (Ghanati et al., 2024).

The macronutrient-based fertilizers effect on oxalate production in plants varies. For instance, the question about nitrogen-role in oxalate synthesis still remains unclear. Conversely, manure containing potassium has shown a correlation with higher oxalate content in *Pennisetum purpureum*. Furthermore, information on the effect of phosphorus fertilization on oxalate levels in forage is still lacking, although superphosphate application has been observed to reduce oxalate levels in vegetables (Rahman & Kawamura, 2011).

7 Risks Assessment with Excessive Oxalate Consumption for Animals and Humans

Essential nutrients are found in both plant and animal products (Šmehýl & Gondeková, 2022; Kapusniaková et al., 2023), but their absorption differs. Average daily oxalate intake corresponds to 70–150 mg (Ghanati et al., 2024). High oxalate levels could hinder the absorption of mineral nutrients such as iron and calcium and in contrast, meat does not contain oxalates and provides vitamins and mineral nutrients in greatly bioavailable and absorbable species (Liebman & Al-Wahsh, 2011).

Soluble oxalate binds to cations such as Na^+, K^+, NH_4^+, or Mg^{2+}, partly limiting their absorption (Li et al., 2022). At higher concentrations in the rumen or intestine, insoluble oxalate crystals, which cannot be absorbed are periodically excreted in excrements. Ruminants could partially metabolize oxalate through mechanisms involving degradation by rumen (intestinal) bacteria, including *Oxalobacter formigenes*, *Enterococcus faecalis*, and lactic acid bacteria (Campieri et al., 2001, Stewart et al., 2004).

Low calcium intake allows soluble oxalate to be absorbed into the bloodstream. High oxalate levels in the blood could bind with Ca^{2+} or Mg^{2+}, forming insoluble crystals and potentially leading to urinary or gallstones (Massey 2003; Chaudhary et al., 2010).

In severe cases, high oxalate exposure could lead to poisoning where, acute poisoning causes a sudden drop in serum Ca^{2+} levels, impairing cell function and leading to hypocalcemia, muscle tremors, weakness, collapse, and potentially death. The parathyroid hormone (PTH) is usually released in reaction to low blood Ca^{2+}, causing the Ca release from bones. Chronic oxalate poisoning results in calcium oxalate crystals damaging kidney tubules, leading to nephron damage, kidney fibrosis, renal failure, and urolithiasis (Ghanati et al., 2024).

8 Conclusion

The Part I of the critical mini-review evaluated strategies, principles, and conditions for the formation and evolution of biominerals, exploring the diversity in different microorganisms and organisms and applications across classical academic fields such as paleontology, paleoecology, and climate studies. By examining mechanisms of biologically induced extra- and intracellular crystallization, we highlight "self-assembly" as a promising approach for future technological challenges and solutions including bionanotechnology.

In exploring the genesis and phytolith cycling in plants, we discuss water-soluble oxalic acid and thermodynamically more stable, insoluble oxalates, which are among the most common in animal and human plant-based diets. This is especially significant because of the long-term excessive intake potential, their distribution with undesirable reactivity, reduced macro- and micronutrients bioavailability with potential toxicity.

We provided a comprehensive overview of oxalates, covering their presence in plants, physicochemical and biological properties, distribution, and potential risks associated with excessive intake. Understanding their significance is increasingly relevant in agronomy, veterinary and medical science. The second part of this mini-review will address the classification challenges, formation factors, and agronomical roles of the second most common phytolith – silicon dioxide in opal form.

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