Physiological and ecological significance of biomineralization in plants

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Biomineralization is widespread in the plant kingdom. The most common types of biominerals in plants are calcium oxalate crystals, calcium carbonate, and silica. Functions of biominerals may depend on their shape, size, abundance, placement, and chemical composition. In this review we highlight advances in understanding physiological and ecological significance of biomineralization in plants. We focus on the functions of biomineralization in regulating cytoplasmic free calcium levels, detoxifying aluminum and heavy metals, light gathering and scattering to optimize photosynthesis, aiding in pollen release, germination, and tube growth, the roles it plays in herbivore deterrence, biogeochemical cycling of carbon, calcium, and silicon, and sequestering atmospheric CO2.

Biomineralization in plants

Biomineralization (see Glossary) occurs in most organs and tissues within plants [1–4]. Commonly reported biominerals in plants are calcium oxalate (CaOX) crystals [5–8], calcium carbonate (amorphous CaCO3 or calcite) [9–11], and amorphous silica [12–14]. Calcium sulfate [15–18], calcium phosphate [19], magnesium oxalate [15,20,21], strontium oxalate [20,22], and strontium and barium sulfate [16,20,23] have been observed in some plant species. Metals such as sodium, potassium, aluminum, iron, manganese, cadmium, and zinc are also found in biominerals in some plants [10,20,24–28], indicating that the chemical composition of biominerals in plants is diverse.

There are several hypotheses to the functions of biomineralization in plants, including regulating cytoplasmic calcium levels, detoxifying aluminum and heavy metals, gathering and scattering light, aiding in pollen release and germination, alleviating water, salt, and temperature stress, regulating ion balance (e.g., sodium and potassium), detoxifying oxalic acid, disposing of alkalinity generated by nitrate assimilation in above-ground organs, protecting plants against herbivory and pathogen attack, providing tissue rigidity and mechanical support, and guiding positively gravitropic growth of the rhizoids of charophycean algae [1–3,13,17,19,23,29–32].

Glossary

Biogeochemical cycle: a circuit or pathway by which a chemical element or molecule moves through both biotic and abiotic compartments of an ecosystem. While all elements are recycled, in some such cycles there may be sinks where the elements are accumulated or held for a long period of time.

Biomineralization: the process by which organisms form minerals. The formation of biominerals may be “biologically induced” or “biologically controlled”. “Biologically controlled” is also termed “matrix-mediated”. In “biologically induced” mineralization the organism modifies its proximal environment and creates physicochemical conditions favoring mineral precipitation; the process is promoted by the organism but the organism has little or no control over the localization, orientation, morphology, or composition of the crystals, and no specific biomolecules or organic matrices are involved in the processes. By contrast, in “biologically controlled” mineralization the localization, nucleation, growth, shape, and size of crystals are controlled by the organism, and organic matrices made up of proteins, polysaccharides, proteolipids, and proteoglycans produced by the organism are responsible for the control.

Coccolithophores: a group of unicellular marine phytoplankton which produce minute calcite plates, termed coccoliths, around each living cell as an outer covering or scales. Coccoliths are typical “biologically controlled” biominerals.

Cryo-SEM-EDX: Cryo-scanning energy-dispersive X-ray microanalysis, a technique used to determine the distribution and concentration of elements in situ at the level of individual cells and sometimes within cell organelles, in which bulk tissues are rapidly frozen in liquid nitrogen (termed cryo-fixation), and the shapes and dimensions of hydrated structures are retained in situ from life to examination in the SEM.

Cystolith: amorphous calcium carbonate in plants.

Druse: a crystal conglomerate that is thought to be formed by precipitation of multiple crystals around a nucleation site.

EDX: energy-dispersive X-ray microanalysis.

Frustule: the hard and porous cell wall or external layer of diatoms, which is composed of very pure hydrated silica.

Phylloclades: modified petioles that function as leaves.

Phyloplankton: usually refers to amorphous silica formed in plants, also termed silicic phytoplankton or opal phytoplankton, although in some cases it is used to describe all biominerals in plants.

SEM: scanning electron microscopy.

Thiophore: a plant with a leaf sulfur concentration ranging from 25 to 82 mg S g⁻¹ dry weight.
In addition to the above-proposed physiological functions, biomineralization in plants is also of ecological significance [33] and it is this aspect that we will focus on in this review. In fact, a field of research on the role plants play in biogeochemical cycles via biomineralization has been developed, including the study of carbon, calcium, and silicon fluxes [34–36]. Here we highlight the physiological significance of biomineralization in calcium regulation, detoxification of aluminum and heavy metals, light regulation, and facilitating pollen release, germination, and tube growth, as well as its ecological significance in herbivore deterrence and biogeochemical cycling of carbon, calcium, and silicon, and sequestering of atmospheric CO₂.

**Physiological significance**

**Calcium regulation**

Calcium is an essential plant nutrient with many fundamental functions in cellular metabolism [37]. In most plants cytoplasmic free calcium required for cellular metabolism is maintained at 10⁻⁷ M or less. Plants often accumulate calcium in excess of cytoplasmic requirements. Excessive free calcium in the cytoplasm is toxic to plants and interferes with several metabolic processes, including calcium-dependent signaling and phosphate-based energy metabolism; therefore cytoplasmic free calcium levels are tightly controlled [4].

Sequestering excessive calcium in a physiologically and osmotically inactive form is an effective way to regulate cytoplasmic free calcium levels and avoiding potential toxic effects. Calcium oxalate crystals are the most common types of biominerals in plants; they account for 3–80% of plant dry weight and up to 90% of the total calcium of a plant, and calcium regulation is one of the most important proposed functions of CaOX [2]. Relative to surrounding mesophyll cells, crystal idioblasts of water lettuce (*Pistia stratiotes*) act as high-capacity calcium sinks, accumulating large amounts of calcium within the vacuole as CaOX crystals [38]. Deposition of CaOX in cells in the vicinity of the stomatal guard cells is responsible for the necessary calcium regulation, and may contribute to the effective stomatal control of gas exchange [39,40]. In some plants, for example duckweed (*Lemna minor*) [6], common bean (*Phaseolus vulgaris*) [2,41], mulberry (*Morus australis*) [42], and Jew's mallow (*Corchorus olitorius*), the production of CaOX crystals increases with increasing calcium concentration in the growth medium, indicating that the formation of CaOX as calcium sinks is inducible [43]. There is also evidence that the formation of CaOX is a rapid and reversible process. Calcium stored in CaOX can be remobilized under conditions when calcium is limiting to plant growth and development [42,44,45]; in such cases CaOX crystals act as calcium reserves. However, there are examples showing that CaOX formation in some tissues and/or plants is not inducible by changes in soil calcium availability [46,47].

The formation of CaCO₃ is another component of calcium metabolism; for example, in leaves of mulberry the size of individual amorphous CaCO₃ depositions increases with increasing calcium concentration in the growth medium. However, the formation of CaCO₃ may play a less-important role in calcium regulation than CaOX does in mulberry leaves because its formation is less responsive to changes in calcium supply [42]. It is necessary to study the formation of CaOX and CaCO₃ in response to calcium supply in a comparative way on more plant species to clarify which of the two types of calcium biominerals is more closely linked with calcium regulation.

Other types of calcium biominerals such as calcium sulfate may also play an important role in calcium regulation in certain plants; for example, robe’s wattle (*Acacia roebeorum*) native to the Great Sandy Desert in northwestern Australia has a large amount of calcium sulfate crystals in its phylloids (Figure 1) and branchlets [15]. Concentrations of calcium, magnesium, and sulfur in the phylloids of robe’s wattle are 72, 10, and 42 mg g⁻¹ (dry weight), respectively [15]; this species can be identified as a thiophore [48]. The sulfur and magnesium crystals may serve as sulfur and magnesium sinks, and regulate sulfur and magnesium levels in the cytoplasm (Figure 2).

![Figure 1. Phylloides (arrowed) of (A) Acacia roebeorum, (B) Acacia ancistrocarpa, (C) Acacia stipuligera, and (D) Acacia stellaticeps. All scale bars are equivalent to 2 cm.](image-url)
Biogenic formation of calcium sulfate crystals may also explain the high foliar calcium and sulfur concentrations of a few other *Acacia* species in north-western Australia (P. Hayes, B. Turner, H. Lambers, E. Laliberté, unpublished).

**Detoxification of aluminum and heavy metals**

Several studies show involvement of CaOX crystals in aluminum and heavy-metal detoxification. Incorporation of aluminum into CaOX crystals has been observed in leaves of Jew’s mallow [49]. The presence of strontium...
in CaOX crystals has been documented in leaves of duckweed, sugar beet (*Beta vulgaris*), pink fringe (*Arthrostroma ciliatum*), and silky glyce (Glyce canecens) [22]; in leaves of water hyacinth (*Eichhornia crassipes*) [50]; in phyllodes and branchlets of Fitzroy wattle (*Acacia ancistrocarpa*) [20], and in phyllodes of *Acacia stipuligera* and robe’s wattle (Figure 3). Cadmium has been detected in CaOX crystals in leaves of water hyacinth [50] and in various tissues of tomato (*Solanum lycopersicum*) [51]. Crystallization of CaOX may also play a role in lead (Pb) deposition and tolerance in leaves of water hyacinth [50]. However, addition of heavy metals such as zinc and lead decreases the number of CaOX crystals, without inclusion of heavy metals in CaOX crystals in leaves of common bean, suggesting that CaOX crystals do not play a major role in heavy-metal detoxification of this heavy-metal sensitive species [52]. The results of the above-mentioned studies indicate that deposition of heavy metals in CaOX crystals is both metal- and plant species-specific.

Intracellular sequestration of heavy metals such as manganese, zinc, and strontium with CaCO3 has been reported in leaves of Cuban laurel (*Ficus retusa*) [10]. In tobacco (*Nicotiana tabacum*) plants, excretion of cadmium- and/or zinc-substituted CaCO3 grains and other zinc-containing compounds (e.g., zinc organic compounds, zinc-sorbed silica, and zinc-sorbed phosphate) via trichomes is reported a potent detoxification mechanism [28,53,54].

In many plants silicon is mainly incorporated into the cell walls, and coprecipitation of aluminum and heavy metals with silicon in the cell walls may be responsible for the alleviation of their toxicity. Such alleviation of toxicity has been demonstrated by the formation of aluminum silicate in epidermal cell walls of sorghum (*Sorghum bicolor*) [55], white spruce (*Picea glauca*) [56], and maize (*Zea mays*) [57]. In leaves of bladder campion (*Silene vulgaris* ssp. *humilis*), a heavy-metal-tolerant plant growing on the polluted soil of a medieval copper-mining dump, zinc and tin accumulated in cell walls as silicate [58]. Cucumber (*Cucumis sativus*) plants treated with silicon showed a decreased percentage and concentration of symplasmic manganese, and an increased percentage and concentration of manganese bound to the leaf cell walls, resulting in higher manganese tolerance [59]. Simultaneous presence of silica, cadmium, and zinc deposits has been observed in cell walls of epidermis, exodermis, and endodermis of maize roots [60]. Codeposition of aluminum and heavy metals with silica can significantly reduce the apoplastic transport of these metals, thus alleviating their toxic effects on plants [55,60]. Coprecipitation of heavy metals and silicon can also occur in the symplasm; for example, when *Arabidopsis* (formerly *Cardaminopsis*) *halleri*, a zinc- and cadmium-hyperaccumulator, is grown on a zinc- and copper-polluted soil, zinc coprecipitates with silicon and forms zinc silicate in the cytoplasm and nuclei of leaf cells, and the formation of zinc silicate is regarded as part of the zinc-tolerance mechanism of this species [61]. Cadmium and zinc coprecipitate with silicon in the cytoplasm and vacuoles of mesophyll cells when maize is grown on a cadmium- and zinc-enriched soil [60]. In phyllodes of *A. stipuligera* and robe’s wattle, coprecipitation of aluminum and iron with silicon has been observed (Figure 4). There are other mechanisms involved in silicon-mediated aluminum and heavy-metal detoxification in higher plants; these are summarized in earlier reviews [62,63].

Beyond CaOX, CaCO3, and silica, there are other types of biominerals that may contribute to heavy-metal detoxification in plants. In charophycean algae such as desmids and Charales the formation of strontium and barium

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**Figure 3.** Sequestration of strontium (Sr) and barium (Ba) in oxalate and sulfate biominerals formed in phyllodes of four *Acacia* species. (A–D) Scanning electron microscopy (SEM) images of biominerals (arrow) in phyllodes of *Acacia ancistrocarpa*, *Acacia robeerum*, *Acacia stipulignera*, and *Acacia stellaticeps*, respectively. (E–H) Corresponding energy-dispersive X-ray microanalysis (EDX) spectra of biominerals in (A–D). Scale bars: (A), 5 μm; (B), 10 μm; (C, D), 2 μm. Adapted from [20].
sulfates is relatively common [23], even in the presence of an excess of calcium [16]. The desmid green alga (*Closterium moniliferum*) is effective in remediating $^{90}$Sr and cleaning nuclear waste [16]. Formation of sulfate biominerals may play a role in detoxifying heavy metals such as strontium, barium, manganese, and copper in land plants, for example in *A. stipuligera*, glistening wattle (*Acacia stellaticeps*) [20], and robe’s wattle (Figures 3 and 4).

It remains unclear to what degree biomineralization contributes to aluminum and heavy-metal detoxification. The detoxification mechanisms are expected to be elucidated by studying the anatomy, physiology, and molecular biology of the plants in combination, using modern technologies such as Cryo-SEM-EDX to localize aluminum, heavy metals and biominerals in plants, identifying key genes controlling biomineralization, heavy-metal uptake and detoxification, and establishing correlations between expression of these genes and toxicity of aluminum and heavy metals. Isotope/pulse–chase techniques may also be applied to quantify metal ions as a function of time and spatial distribution within plant tissues and/or cells.

**Light regulation**

Light gathering and reflection is one of the proposed functions of CaOX druse crystals [2, 64]. In leaves of six *Peperomia* species, which are low-light-adapted, CaOX druse crystals are specifically produced in the photosynthetic palisade cells rather than in specialized idioblasts, and each palisade cell contains a druse crystal within its vacuole, indicating that the crystals play a role other than calcium regulation in these plants [65]. In cypress peperomia (*Peperomia glabella*) the size of druse crystals in palisade cells decreases with increasing light intensity. The position of the crystals also changes with light intensity, showing that the crystals move up as the light intensity increases. It is hypothesized that the crystals help to distribute light evenly to the chloroplasts. Placing the crystals at the middle or bottom of the cells at low light levels would help distribute the limited light to the chloroplasts towards the bottom half of the palisade cells and maximize light capture; at high light levels crystals formed at the top of the palisade cells may dissipate excess light by reflecting part of the light back up to the window tissue,
thus protecting the shade-adapted chloroplasts from photodamage and minimizing photoinhibition [65,66]. Further support for this hypothesis comes from a study that demonstrated that the refractive indices of cystoliths and CaOX druses in leaves of small-fruited fig (Ficus microcarpa) are significantly higher than those of the surrounding cytoplasm and cell wall, thus the cystoliths and CaOX druses act as light scatterers and reduce the steep light gradient generated by photosynthetic pigments, enabling the leaf to use the incoming light flux more efficiently [67]. The authors also found that the spatial distribution of the biominerals is compatible with their optical function. The above-mentioned results suggest that biominerals are involved in the photosynthetic process in land plants [66,67].

Coccoliths are effective at scattering light, making a coccolithophore bloom easily visible from space by satellite [11]. There is much debate about the role of coccoliths in light scattering in coccolithophores. The optical signature of coccolithophore blooms is largely (80%) a result of the detached coccoliths that are freely floating, rather than the living cells themselves [68]. Whether light scattering by biominerals is common and functionally important in the plant kingdom warrants further critical study.

Facilitating pollen release, germination, and tube growth
Calcium oxalate crystals may facilitate pollen release and germination. In anthers of chili pepper (Capsicum annuum) there are many CaOX crystals in the connective tissue and in the hypodermal stomium between adjacent locules. It has been suggested that calcium is systemically removed from the cytoplasm and cell walls of the connective tissue and the stoma, and is sequestered in CaOX crystals when the pollen matures. This leads to degradation and weakening of the cell walls between the locules, followed by collapse of the connective tissue and the stoma, and thereafter fusion of adjacent locules. Thus, formation of these crystals is believed to aid in anther dehiscence and pollen release [19,69].

Calcium is required for pollen germination and tube growth, and the calcium required is provided by either the stigma or pollen grains, or both [70,71]. In the anther of petunia (Petunia hybrida) many calcium crystals accumulate under the stoma and adhere to pollen grains, and they move to the stigma together with pollen grains when the anther dehices and pollen grains are released. The increase in calcium concentration on the stigma of petunia does not come from the stigma but from the calcium crystals adhered to the pollen grains. Such calcium crystals around the pollen may enhance pollination by providing calcium required for pollen germination and tube growth of Petunia and Nicotiana [29].

To test this hypothesis an extensive survey of the presence of CaOX crystals in anthers and their relation with the pollination strategies of various plants would need to be carried out.

Ecological significance
Herbivore deterrence
There is increasing evidence supporting the contention that biomineralization protects plants against herbivory by insects as well as large animals, and this function is achieved either physically or chemically depending on the shape, size, placement, abundance, and chemical composition of the biominerals [1–3,72].

For a Negev desert lily (Panacratium sickenbergeri), only the leaf parts devoid of CaOX raphide crystals are consumed by dorcas gazelle; comparisons of the abundance of CaOX raphides in different lily populations revealed that the severity of herbivory in different populations correlates negatively with their raphide abundance [46]. In leaves of arrow-leaf sida (Sida rhombifolia) subjected to herbivory [73], CaOX production increases, indicating that formation of CaOX crystals in some tissues and/or plants is an inducible defense response to herbivory. However, it is suggested that the formation of CaOX crystals in some tissues and/or plants is a constitutive rather than induced defense against herbivores. For example, after simulated herbivory by clipping bulbs [74] and leaves [47] of the Negev desert lily, the number of CaOX crystals did not increase significantly. In some conifer species, increased CaOX crystal accumulation in the secondary phloem appears to be antagonistic to beetle attack, suggesting that CaOX crystals functions as a constitutive defense against small bark-boring insects [75]. Constitutive defense may well be a more appropriate strategy than induced defense in environments with unpredictability, especially when leaves are ephemeral and herbivore pressure is high [47].

The deposition of solid hydrated amorphous silica reinforces the cell wall and protects many plants against attacks by herbivores through increasing the abrasiveness and reducing the digestibility of plant tissues [1,76–78]. Plants native to heavily-grazed habitats accumulate more silica than plants native to less-heavily-grazed habitats, and plants attacked by herbivores accumulate more silica than non-attacked plants, indicating that silicification is an inducible defense mechanism against herbivory [79,80]. For perennial ryegrass (Lolium perenne) and sheep's fescue (Festuca ovina), although single attacks do not alter the silica concentration in the regrowth tissue of either species, repeated attacks by either voles or locusts result in over 400% increases in silica concentrations in both species, and the increases deter attacks by both herbivores [81]. Adverse impacts of silica on herbivore performance have been reported. Higher silica levels in grasses reduce the growth rates [77,80] and population density [80] of some herbivores; silica-based defenses in grasses may play a key role in driving population cycles of particular herbivores [80,82], and quantitative heterogeneity of this plant defense system may contribute to the evolution of high species diversity in herbivores [79]. Diatom frustules are remarkably strong to provide mechanical protection for the cells by virtue of their architecture and the material properties of the silica, and the evolutionary arms-race between diatoms and their specialized predators may have considerable influence in structuring pelagic food webs [14].

Contribution to biogeochemical cycles
For CaOX biominerals in plants, calcium is taken up from the soil by roots, and oxalate is biologically synthesized,
using carbon fixed during photosynthesis, and the original source of carbon in biogenic CaOX is therefore atmospheric CO₂ [2,83,84]. Unlike most carbon-based compounds in plants, which break down into their constituent components and release CO₂ back into the atmosphere when plants die, CaOX crystals in plants such as the iroko tree (Milicia excelsa) [34,83], the saguaro cactus (Carnegiella gigantea), and other cacti in arid and semi-arid regions [36,84] are released into the environment and slowly transformed into solid CaCO₃ via the oxalate–carbonate pathway, thus sequestering atmospheric CO₂ into the soil as inorganic carbon. The inorganic carbon has a longer soil residence time than organic carbon; therefore it is suggested that the bio-induced CaCO₃ represents a long-term carbon sink, and the inorganic carbon sink is more efficient for carbon sequestration than soil organic matter, provided that the calcium originates from non-carbonate minerals such as calcium-containing silicates [83–85]. In addition, when plants mobilize nutrients from silicates in soils, atmospheric CO₂ is consumed and converted to bicarbonate, and sequestered in soils as carbonates; even if CO₂ is produced when bicarbonate is transformed into carbonate there is net CO₂ sequestration [86–88]. Given that the formation of CaOX biominerals is common in the plant kingdom, and that CaCO₃ accumulation is observed in soils where it is not expected to take place, biomineralization of CaOX may have locally significant impacts upon carbon and calcium cycling [36,84,86,89]. Biomineralization of CaOX in plants is especially important for the carbon cycle in arid environments where soil organic carbon contents are low [36].

Coccolithophores play an important role in carbon and calcium cycling in the oceans. Through photosynthesis and calcification, dissolved inorganic carbon is transformed into particulate inorganic carbon (CaCO₃) and organic matter which sink towards the ocean floor, where coccoliths are the largest single component of deep-sea sediments. The precipitation of coccoliths constitutes a sink of carbon and calcium, although calcification produces CO₂ [90,91].

Some studies have demonstrated that biogenic silica is an important component of the biogeochemical cycle of silicon [35,87,92–97]. Amorphous silica formed in plants can be released into the environment and accumulates in soils after plant death because it is more resistant to decomposition than other plant tissues [93,96]. Dissolved silicon released from soil mineral silicates and silica phytoliths stored in the soil is either taken up by plants or transported to rivers and oceans, and used by the aquatic ecosystems in which diatoms, the most evident biological silicon sink, take up dissolved silicon and deposit it as amorphous silica. Rapid recycling of diatom silica and silicon import from land are crucial for the diatom-based food webs [87,94]. Because of its greater chemical mobility than that of mineral silicates and crystalline silica phases, biogenic amorphous silica plays a major role in the cycling of silicon in soils and aquatic environments [86,93,94]. It is estimated that the phytolith silica fixed annually by terrestrial plants is of the same order of magnitude as that fixed in the oceanic biogeochemical cycle [35], and both the terrestrial and oceanic silicon cycles are driven by recycling of amorphous silica [94]. The role that biogenic amorphous silica plays in the biogeochemical silicon cycle has been discussed in earlier reviews [35,87,94,96].

Biosequestration of carbon within phytoliths has been reported in a few plant species and/or cultivars, including economic bamboo species [98], and different wheat (Triticum sp.) [99] and rice (Oryza sativa) [100] cultivars. The phytolith-occluded carbon is a relatively stable form of organic carbon, it can accumulate in soils after decomposition of plant tissues [101], and it is regarded as a mechanism of long-term biogeochemical carbon sequestration [100].

The above-mentioned biomineralization in plants plays an important role in biogeochemical cycling of carbon, sequestering a significant amount of atmospheric CO₂. More work is necessary to gain knowledge on the role that biomineralization in plants may play in mitigating the greenhouse effects on global climate change. Crystals of CaOX are widespread in angiosperms, including both dicotyledons and monocotyledons [102], but biogenic silica is much more common in monocotyledons, especially in grasses of the Gramineae family, than in dicotyledons, according to existing literature, and silicon concentrations of monocotyledons (1–15% of shoot dry weight) are generally higher than those of most dicotyledons (no more than 0.5% of shoot dry weight) [35]. Studies on the biogeochemical cycling of carbon, calcium, and silicon in various ecosystems with different vegetation types (i.e., vegetation made up of plants with different accumulation patterns of calcium and/or silicon biominerals) would further clarify the effects of biomineralization on cycling of these elements, and provide a theoretical basis for ecosystem conservation and vegetation design of ecosystems that require restoration.

**Concluding remarks and future directions**

In summary, biomineralization is common in plants and the chemical composition of biominerals is diverse. Functions of biominerals may depend on their shape, size, abundance, placement, and chemical composition. Increasing evidence supports the physiological significance of biomineralization in the regulation of cytoplasmic free calcium levels, the detoxification of aluminum and heavy metals, gathering and scattering light to optimize photosynthesis, and aiding in pollen release, germination, and tube growth. The role biomineralization plays in protecting plants against herbivory and its contribution to the biogeochemical cycles of carbon, calcium, and silicon demonstrate that biomineralization is also of ecological significance.

Studying the physiological and ecological significance of biomineralization requires multidisciplinary collaboration. Future work should closely link anatomical and physiological studies to molecular mechanisms to gain a thorough insight into the physiological significance of biomineralization. Plant scientists and earth and marine scientists are expected to join forces to elucidate the role biomineralization plays in ecosystems, especially in sequestering atmospheric CO₂ to mitigate the greenhouse effects on global climate change.
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