

IRON BIOGEOCHEMISTRY AND ITS ENVIRONMENTAL IMPACTS IN FRESHWATER LAKES

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ABSTRACT

Iron is an essential element for almost all living species. Its environmental impacts on physiology and ecology of aquatic organisms are always the focus of limnology and oceanography. To gain insight into iron biogeochemistry and its environmental impacts in freshwater lakes, we collected and reviewed numerous studies on iron in combination with our own work. Our review reports iron sources, iron speciation, iron cycle and iron uptake mechanisms as well as impacts of iron on physiology and ecology of phytoplankton and aquatic plants in freshwater lakes. We also proposed some suggestions for further studies.

KEYWORDS: iron biogeochemistry, freshwater lakes, iron speciation, size-fractionated iron, iron uptake mechanisms

1. INTRODUCTION

Iron is the second most abundant metal and fourth most abundant element in the Earth's crust [1], but its concentration in water is quite low because of low solubility [2, 3]. Generally, iron concentrations in natural freshwaters do not exceed 1 mg L^{-1} [4]. However, population explosion, rapid urbanization and growth of industries result in various ecological problems in the ecosystems of most water-bodies. Lakes act as a recipient of wastewaters like a dustbin, which leads to eutrophication and algal blooms. As a consequence, significant changes in speciation, concentration and bioavailability of iron in lake water and sediment occur [5-7]. Conversely, variations of iron profoundly influence the structure and function of lake ecosystems [3]. Therefore, iron biogeochemistry and its environmental impacts in freshwater lakes are always the research focus in limnology. The review consists of iron sources, iron speciation, iron cycle, iron uptake mechanisms and impacts of iron on physiology as well as ecology of phytoplankton and aquatic plants in freshwater lakes.

2. IRON SOURCES IN FRESHWATER LAKES

There are many iron sources in freshwater lakes. In natural conditions, iron primarily comes from the products of weathered rocks and soil around watersheds, controlled by many factors, such as geological process, soil composition, environmental temperature, precipitation, and hydrology [8]. Another important contributor is air deposition [9-12]. Some nutrient elements, like nitrogen, phosphorus, sulphur and iron, can fall into lakes with precipitation and dust, or simply due to gravity. More important, wastewater and storm-water discharges have already been the first source of iron in freshwater lakes because of anthropogenic influences [5].

3. IRON SPECIATION AND IRON CYCLE

Numerous studies about iron speciation in freshwater lakes have been carried out. However, most studies have focused on redox reactions at oxic/anoxic boundaries in water columns [13-17]. The redox transformations at the oxic/anoxic boundary influence the iron cycle in lakes because of the solubility difference between ferrous (Fe^{2+}) and ferric (Fe^{3+}) iron [4]. In oxic waters, ferric iron is the stable oxidation state and, at neutral pH, it forms highly insoluble oxides and hydroxides [4, 16, 17]. Ferrous iron is stable in anoxic waters and, in many freshwater systems, it exists usually as a dissolved ion, although, in the presence of high carbonate, sulphide and orthophosphate levels, it forms insoluble salts [18]. Most studies showed that reduction of ferric iron can also occur in oxygenated, high pH, surface lake waters, although this usually results in much lower concentration of ferrous iron [19-21]. These redox reactions would enhance iron availability to phytoplankton and aquatic plants by releasing organically bound Fe (Fe^{3+}) [22], or upon reoxidation.

However, iron speciation is highly affected by the chemical composition of the lake water, iron inputs and removal processes, as well as internal recycling [13]. The physicochemical speciation of iron, which profoundly influences its bioavailability, depends on the relative importance of various competing processes including adsorption-desorption, precipitation-dissolution, ion exchange, complexation-dissociation, and redox reactions [3]. Hence, the

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traditional classification of iron speciation could not satisfy the demand of collecting information on iron biogeochemistry in presently complex lakes anymore.

The following method based on size separation has been accepted and applied in limnology. Operationally defined filtration and ultra-filtration techniques set boundaries in the continuum between dissolved, colloidal and particulate phases. Accordingly, iron in lake water is separated for three size fractions: particulate iron ($>0.22\ \mu\text{m}$), colloidal iron ($0.025\text{--}0.22\ \mu\text{m}$) and soluble iron ($<0.025\ \mu\text{m}$) [3, 5-7, 23, 24]. The highly reactive colloidal iron may either coagulate or flocculate to form larger particles, or become soluble [18, 25]. In addition to controlling iron solubility, the formation of colloidal and larger, more refractory iron particles provides a mechanism for removing dissolved iron and other trace metals from the water by adsorption and co-precipitation [18]. Bioavailable iron has been studied clearly, but the cycle involving the new iron speciation is not well understood.

According to the above new method, experiments of iron separation were conducted in Dianchi Lake (China) [5-7]. Concentrations of size-fractionated iron in lake water were much higher than that in other lakes (e.g. Kinneret Lake, Israel) and varied with season because of serious cyanobacterial blooms in summer and autumn. Similar to the view of Shaked et al. [3], we found that size-fractionated iron could transform into each other, especially the highly reactive colloidal iron [5-7], and significant linear correlations were found between iron in different size fractions [5].

4. IRON UPTAKE MECHANISMS OF PHYTOPLANKTON AND AQUATIC PLANTS

Iron availability to organisms depends on (1) total concentration of iron, (2) its chemical speciation, and (3) how the physicochemical properties of a system alter that speciation [26].

4.1. Iron uptake mechanisms of phytoplankton

Phytoplankton differs from land-based plants in that they do not have roots, stems, or leaves. But the whole body of phytoplankton can take up nutrients from ambient environment. There are many studies on iron uptake mechanisms of phytoplankton, but there is little information about freshwater phytoplankton used as experimental material compared to oceanic phytoplankton.

Possible uptake mechanisms of freshwater phytoplankton are as follows:

4.1.1. Iron uptake through membrane transport

The mechanism includes two steps. First step is a passive adsorption process, that is, physical adsorption or ion exchange occurs on algal cell surface. Moreover, no energy is consumed and very short time is needed in the

step. Second step is an active absorption process. Because it is related to metabolisms of organisms, thereby, large amount of energy is consumed [27].

Importantly, ferric iron (Fe^{3+}) must transform into ferrous iron (Fe^{2+}) before it can be absorbed in the pathway. Fe^{2+} is then transported into phytoplankton cells through special transport points on the membrane [28]. The mechanism may be a main pathway for freshwater phytoplankton, especially cyanobacteria [27].

4.1.2. Iron uptake through Fe^{3+} -siderophores

Siderophores are organic Fe^{3+} /metal-chelating molecules that serve to solubilize and scavenge Fe^{3+} from ambient environment. They are classified as phenolates-catecholates or hydroxamates, or mixtures of the two forms [29]. The Fe^{3+} -siderophore complex is subsequently imported into the cell. Most freshwater phytoplankton, especially cyanobacteria, can secrete siderophores under iron-limited environment [30-34]. Lammers and Sanders-Loehr [30] proved that some strains of *Anabaena* can produce schizokinen (a siderophore). Besides *Anabaena*, *M. aeruginosa* can also produce hydroxamate-type siderophores [32]. In our previous study, siderophores were found in culture solutions of *M. aeruginosa* and *M. wesenbergii* isolated from Dianchi Lake (China) [34]. Furthermore, the amount of siderophores of *M. aeruginosa* was much more than that of *M. wesenbergii*, as *M. aeruginosa* requires a higher iron concentration than *M. wesenbergii* [34].

4.1.3. Iron excess absorption and storage

Most phytoplankton species have the ability to excessively absorb (luxury consumption) and store nutrients, especially phosphate under good environment [35]. When times get tough, the storage nutrients would be used by phytoplankton to keep normal metabolisms. But studies on luxury consumption of iron are rare. Wang et al. [36] indicated that iron contents of two strains (a unicellular strain of *M. aeruginosa* PCC7806 and a colonial strain of *M. aeruginosa* XW01) were less than 1/3 cultured in iron-limited than in iron-replete conditions.

4.2. Iron uptake mechanisms of aquatic plants

It is well-known that roots are the main absorbing organs for water and nutrients from environment. Most aquatic plants have an active transpiration-mediated root-pressure system which can transport water and dissolved nutrients from roots through stems to leaves [37]. Moreover, leaves or/and stems of some aquatic plants, such as submerged macrophytes, can also absorb nutrients from ambient environment. Gentner [38] had used $^{59}\text{Fe}^{3+}$ as a tracer to study uptake and transportation of iron in *Vallisneria spiralis* L.. Data showed that roots take up more iron than shoots, and transport within the plant occurs principally in the shoot to root direction [38]. In addition, nutrient concentrations in aquatic plants are far higher than necessary concentrations of metabolisms due to active absorption [37].

Roots of aquatic plants mainly take up iron from lake sediment. Meanwhile, leaves and stems can also absorb iron from water column. But their absorption processes are identical with iron transport into cells of aquatic plants through transferrin [39]. Transferrin binds extracellular iron with high affinity, docks at transferrin receptors on the cell membrane, and is taken up into cells by means of the invagination of sections of this membrane. The iron is then unloaded from transferrin into specialized intracellular compartments, from where it can be transferred to the cytoplasm [29]. In addition, aquatic plants also have the ability to produce siderophores (phytosiderophores, PS) which can retrieve adequate amounts of iron from sediment or/and water [40]. This chelation strategy is more efficient than the reduction strategy used by other plants.

5. EFFECTS OF IRON ON PHYSIOLOGY OF PHYTOPLANKTON AND AQUATIC PLANTS IN FRESHWATER LAKES

As it is well-known, iron is an essential trace element for biological requirements of phytoplankton and aquatic plants. It can be involved in chlorophyll pigment biosynthesis, in many components of photosynthesis (PS I and PS II) and electron transport systems, as well as in nitrate assimilation as an enzyme cofactor (nitrate reductase and nitrite reductase) [41, 42]. Therefore, only good iron concentration promotes growth and physiological metabolisms of phytoplankton and aquatic plants [34, 43-47]. The physiological features determined in studies are generally as follows: growth rate, pigment content, photosynthesis, respiration, nutrient contents, enzyme activities (e.g. nitrate reductase, antioxidant enzymes) and others.

5.1. Phytoplankton

Different phytoplankton species have different thresholds of iron concentration for growth [32, 48]. Sun et al. [48] found that a Fe concentration of 10^{-8} to 10^{-7} M is the threshold for growth of *Anabaena circinalis* (cyanobacterium). Iron stress can inhibit photosystem II (PS II) photochemistry, the amount of photooxidizable reaction center pigment of photosystem I (PS I) (P700), and the partial reaction rates associated with PS II and PS I, respectively [49, 50]. Concomitantly, a large decrease in the amount of phycocyanin (PC) and Chl *a* accompanied by structural alterations of the thylakoid membranes and phycobilisomes as well as a blue shift of 5-6 nm in the main red absorption band of Chl *a* are characteristics of iron-stressed cyanobacteria [51]. Furthermore, the number of iron-containing proteins within the photosynthetic apparatus reduces because of iron limitation [49]. In our previous study, iron limitation ($0.01 \mu\text{M Fe}^{3+}$) seriously affected the growth, pigment content and photosynthesis of *M. aeruginosa* and *M. wesenbergii* [34].

Oxidative stress induced by iron starvation could be a common feature of photosynthetic bacteria [52]. Latifi et al. [52] pointed out that iron deficiency causes oxidative

stress in the cyanobacterium *Anabaena* sp. strain PCC 7120. In addition, iron limitation inhibited remarkably the activities of ATPases (Ca^{2+} -ATPase, Mg^{2+} -ATPase), nitrate reductase (NR) as well as acid phosphatase (ACP) and alkaline phosphatase (ALP) of *M. wesenbergii* [45].

5.2. Aquatic plants

Compared to phytoplankton, studies on effects of iron limitation or iron deficiency on aquatic plants are not fully understood. Most studies focused on phytoremediation of aquatic ecosystems which suffered from contaminations of iron and other heavy metals [46, 47, 53-56]. Therefore, high capacity of metal accumulation with normal physiological metabolisms is a hot topic of phytoremediation using aquatic plants in aquatic environments [53, 56].

Duckweed is a suitable plant model because of its small size, rapid growth, and ease of culture [46, 57, 58]. *Lemna minor* L., *Lemna paucicostata* Hegelm., *Lemna gibba* L. and *Spirodela polyrrhiza* (L.) Schleid are all widely used in toxicity evaluation experiments. In our previous study, *S. polyrrhiza* was used to evaluate its physiological responses to excess iron (1, 10, and $100 \text{ mg L}^{-1} \text{ Fe}^{3+}$, added in the form of $\text{FeCl}_3 \cdot 6\text{H}_2\text{O}$) [46]. After a 24-h short-term exposure, 10 and $100 \text{ mg L}^{-1} \text{ Fe}^{3+}$ caused plants necrosis or death and colonies disintegration as well as roots abscission. Moreover, significant differences in chlorophyll fluorescence (Fv/Fm) were observed at 1-100 mg L^{-1} iron. Furthermore, the synthesis of chlorophyll and protein as well as carbohydrate, and the uptake of phosphate and nitrogen, were inhibited seriously by excess iron. In addition, with the increase of iron concentration, malondialdehyde (MDA) content increased, but proline content decreased.

Though submerged macrophytes and emergent plants are extensively studied, effects of iron on physiology of them are relatively rare. At higher iron solution concentrations, plants exhibit visual symptoms of possible iron toxicity, including root flaccidity, reduced root branching, increased shoot die-back and mottling of leaves [44, 59, 60]. Moreover, Basiouny et al. [43] pointed out that contents of iron and chlorophyll in *Hydrilla verticillata* (L.f.) Royle increased with the increase of iron concentration (0-8.0 ppm). Batty and Younger [44] found a threshold of iron concentration (1 mg L^{-1}) above which seedling growth of *Phragmites australis* was severely inhibited. In addition, *P. australis* is proposed as a more appropriate biological indicator of iron and manganese pollutions [61]. Like phytoplankton, the activities of antioxidative enzymes in aquatic plants, such as *Elodea nuttallii* (Planch.) H. St. John, are inhibited seriously by high iron concentration (beyond $10 \text{ mg L}^{-1} [\text{Fe}^{3+}]$) [47].

6. EFFECTS OF IRON ON ECOLOGY OF PHYTOPLANKTON AND AQUATIC PLANTS IN FRESHWATER LAKES

Since "Iron Hypothesis" has been proposed [62], effects of iron on ecology of phytoplankton in ocean and

fresh water are always research focus in limnology and oceanography [3, 6, 21-24, 63-65]. Though less comprehensively than in the ocean, iron influences algal productivity and species composition in freshwater lakes [3, 66, 67]. It is reported that when iron concentration ranges from 0.1 to 1.0 mg L⁻¹, algal community in lakes shifts from green algae to cyanobacteria [66]. Pollinger et al. [67] also found that iron addition affects species composition of phytoplankton in Lake Kinneret, and markedly promoted the growth of green algae and bacteria. In an *in situ* experiment in Lake Erken (Sweden), phosphate and nitrate were added to all enclosures, but *Gloeotrichia echinulata* only increased in abundance in enclosures to which iron had also been added [68].

Our mimic experiment in enclosures on lakeshore of Dianchi Lake (China) revealed a positive relationship between the decrease of dissolved iron and the increase of biomass of aquatic organisms (submerged macrophytes and bloom-forming cyanobacteria) in the period of June-September [23]. It has been a common phenomenon that dissolved iron concentration is relatively low in summer because of rapid reproduction of phytoplankton, particularly bloom-forming cyanobacteria [23, 69]. However, at the whole-lake scale, iron had no obvious influences on formation of cyanobacterial blooms in shallow and eutrophic Dianchi Lake [6].

For aquatic plants, long-time iron accumulation and iron toxicity could change physiology and ecology of them, such as morphology, anatomy, life-history traits, species composition and community dynamics. Stanković et al. [70] evaluated iron contents in the most common submerged and floating aquatic plants (*Ceratophyllum demersum* L., *Myriophyllum spicatum* L., and *Nymphoides flava* Hill.) of Provala Lake, and iron contents in submerged species were considerably higher than in floating ones, and this may be a reason for degradation of submerged macrophytes. Van der Welle et al. [71, 72] proved that iron profoundly influences species composition and distribution of wetland plants.

Iron plaque is commonly formed on the roots of aquatic plant species, such as *Typha latifolia* L. and *Phragmites australis* Trin. The iron plaque may be amorphous or crystalline [73]. It is composed mainly of ferrihydrite (63%) with lesser amounts of goethite (32%) and minor levels of siderite (5%) [74, 75]. The effect of iron plaque on plant uptake of nutrients and/or contaminants may depend on the amount of iron plaque that is formed on the plant roots [75, 76]. Interestingly, the amount of iron in root plaque is not related to the amount of iron taken up to the shoot, and toxicity symptom expression is not related to root iron plaque [44]. Iron plaques may also act as a nutrient reservoir in times of deficiency that help to solubilize nutrients with restricted availability by acidification [77].

7. PERSPECTIVE OF RESEARCH ON IRON IN FRESHWATER LAKES

Though iron cycle and its impact on phytoplankton and aquatic plants in freshwater lakes are completely reviewed here, some aspects of iron biogeochemistry in freshwater lakes are still not clear. Therefore, based on the review, the following questions of iron are suggested to pay more attention in further studies:

- (1) size-fractionated iron cycle in lake ecosystems;
- (2) bioavailability of different iron speciation and regime shifts of freshwater lakes;
- (3) iron uptake mechanisms and detailed transport pathways at various levels;
- (4) iron biogeochemistry and global climate change.

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