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Review 综 述

红树林沉积物中微生物驱动硫循环研究进展

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摘要：红树林滨海湿地是在周期性咸水、淡水作用下形成的特殊生态系统，其沉积物中有机质含量丰富，微生物驱动的营养物质循环活跃。由于红树林沉积物中硫酸盐含量高、硫化物种类多，因此红树林是研究硫元素生物地球化学循环过程和机制的理想系统。本文综述了红树林生态系统中主要的硫元素循环过程，重点总结了硫氧化和硫酸盐还原过程及其功能微生物，分析了影响硫氧化和硫酸盐还原的主要环境因素，并对红树林沉积物中微生物驱动硫循环的重点研究方向进行了展望。鉴于微生物驱动的硫循环过程耦合碳、氮和金属元素循环，本文可为深入探究微生物驱动的生物地球化学元素循环耦合机制提供参考。

关键词：红树林，沉积物，微生物群落，硫氧化，硫酸盐还原，耦合过程

红树林湿地分布在热带和亚热带的潮间带，主要由红树植物和半红树植物为主的常绿灌木和小乔木组成，是一种连接陆地和海洋的特殊生态系统[1]。在目前已知的各类生态系统中，红树林湿地是最具生产力的生态系统之一[2]，其特点是有机物质和养分周转率高。微生物作为红树林物质循环的重要驱动者[3]，在创造和维护这个生物圈的过程中扮演着非常重要的角色[4]。在过去的几十年里，红树林生态系统在各种人类活动的影响下(如森林砍伐、煤矿开采、城市和工业废物肆意排放和原油泄漏等[5–7])，受到了很大的挑战[8–9]。为适应这些影响带来的环境改变，红树林沉积物中的微生

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物已经演变成适应多种有机和无机污染物的复合功能型微生物[10–11]。有研究表明，微生物结构变量的差异与环境功能变量的差异显著相关[12–13]。因此，微生物群落结构的组成在一定程度上能反映红树林生态系统的生态学功能[14–15]。

红树林作为海陆过渡地带的典型湿地生态系统，其沉积物环境通常具有贫氧、高硫和富营养等特征[16]。红树植物的含硫量通常高于同地带非红树林生态系统中的其他灌木[17]，这对红树林沉积物的结构和性质都具有重要影响[18]。微生物在硫循环过程中驱动氧化还原反应，其中氧、碳和铁是主要的反应物，这导致了这些元素循环相互耦合[19]。微生物驱动的硫酸盐还原及其相关化学反应被认为是控制红树林沉积物化学环境的关键过程[20]。本文主要综述红树林沉积物中微生物驱动的无机硫化合物之间的迁移转化，为更好地认识红树林中微生物驱动的硫循环机制提供理论参考。

1 红树林沉积物中微生物驱动的硫循环过程

红树林沉积物中普遍富含硫，主要以黄铁矿(80%的 Fe 以 FeS_2 赋存)和硫酸盐(SO_4^{2-})形式存在[16]。SO_4^{2-}是红树林沉积物内有机物氧化反应中仅次于 O_2 的重要氧化剂。由于沉积物中共生的大量底栖生物和红树植物发达的呼吸根消耗了 O_2，随着沉积物深度的增加，生物可利用的 O_2 浓度逐渐降低[21]。在有氧层，O_2 是最重要的氧化剂，有机物的降解主要通过微生物的有氧呼吸来实现；而在缺氧层，SO_4^{2-}是最重要的氧化剂，有机物主要通过微生物驱动的硫酸盐还原来分解[22]。微生物能够将包括还原反应产生的硫化氢(H_2S)在内的硫化物(HS^-/S^{2-})氧化为单质硫(S^0)，然后 S^0 歧化为 SO_4^{2-}和 HS^-/S^{2-}[23]，从而形成了硫元素的无机代谢循环(图 1)。此外，微生物也会驱动有机硫化合物

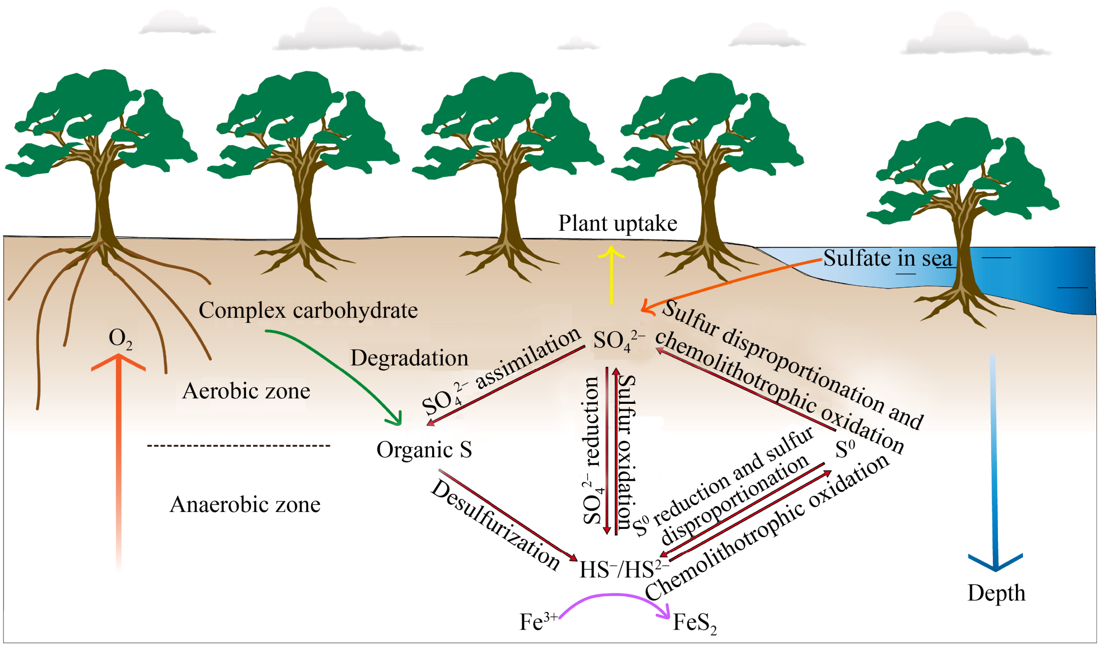

图 1. 红树林沉积物中硫元素的生物地球化学循环

Figure 1. Biogeochemical cycle of sulfur in mangrove sediments.

之间的转化，例如二甲基亚砜(DMSO)可以通过微生物转化为二甲基硫醚(DMS)，反之亦然[24]。

1.1 微生物驱动的硫氧化过程及其影响因素

1.1.1 微生物驱动的硫氧化过程：硫氧化过程是指将低价态的单质硫或还原性硫化物完全氧化为硫酸盐或部分氧化成更高价态的硫化物[25]，主要包括硫化物氧化、单质硫氧化、硫代硫酸盐氧化以及亚硫酸盐氧化[26](图 2)。其中硫化物氧化是指硫氧化菌(sulfur-oxidizing bacteria，SOB)中硫化物氧化酶将 HS^-/S^{2-}氧化成 S^0 的过程。由于 H_2S 等硫化物影响红树林沉积物中动植物的正常生命活动[27]，因此 SOB 在沉积物的硫化物解毒中起着重要作用。单质硫氧化是指 S^0 在 SOB 中反向异化硫酸盐还原酶作用下被氧化成亚硫酸盐(SO_3^{2-})的过程。硫代硫酸盐氧化是指硫代硫酸盐($S_2O_3^{2-}$)在碱性或者中性条件下被 SOB 氧化成 SO_4^{2-}；而在酸性条件下 $S_2O_3^{2-}$被氧化成连四硫酸盐($S_4O_6^{2-}$)[28]。亚硫酸盐氧化是指 SO_3^{2-}在亚硫酸盐氧化酶的作用下被氧化成 SO_4^{2-}。在红树林沉积物的有氧区，硫氧化过程由耗氧 SOB 进行有氧氧化完成[29]；在缺氧区硫氧化过程主要由光养或化能 SOB 利用光能营养或化学能营养进行厌氧氧化完成[30]。但是在缺氧区由于底栖动物的扰动致使微生境局部含氧，因此在缺氧区可能也存在部分耗氧微生物参与硫氧化。

已报道的 SOB 主要分布在绿菌纲(*Chlorobia*)、绿弯菌纲(*Chloroflexi*)、α-变形菌纲(*Alphaproteobacteria*)、β-变形菌纲(*Betaproteobacteria*)、γ-变形菌纲(*Gammaproteobacteria*)等[31–32]。红树林生态系统中孕育着丰富的 SOB (表 1)。如 Liang 等[33]在中国深圳福田红树林沉积物中发现了一些自由生活和共生的 SOB：杆状色菌属(*Rhabdochromatium*)和 *Thioalkalivibrio denitrificans* SOB 自由生活，γ-变形菌纲 SOB 与双壳类满月蛤总科(*Lucinacea*)共生；Zhao 等[34]在中国福建泉州红树林中发现 1 种能广泛利用多种碳、氮和硫物质的海洋紫色硫细菌(*Marichromatium gracile*)新菌株 YL28。在巴西原始红树林被原油泄漏污染的沉积物中，SOB 有较高的多样性，污染样品中检测到的 OTUs 的数量显著高于未污染样品，其中报道了着色菌目

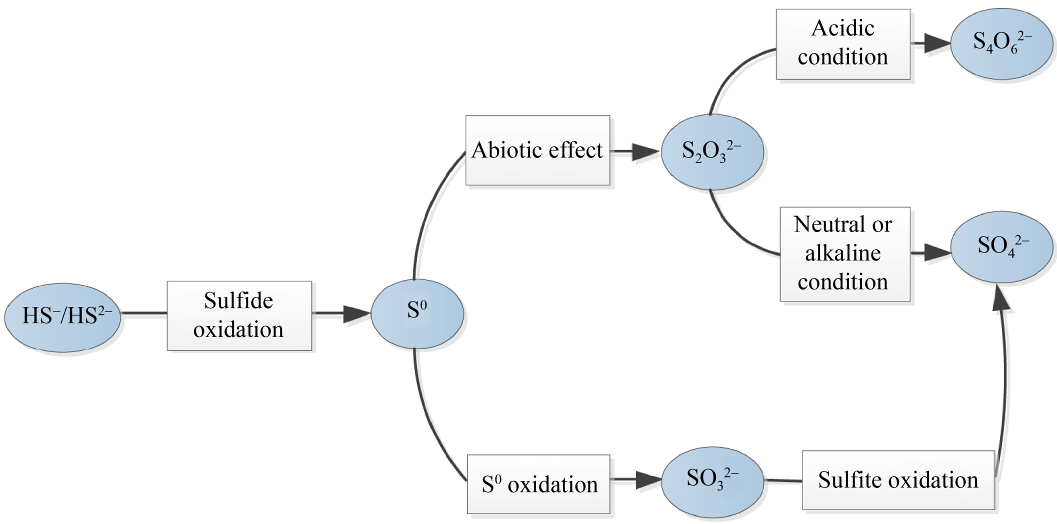

图 2. 微生物驱动的硫化物代谢过程

Figure 2. Schematic illustration of the metabolism of inorganic sulfur compounds by sulfur oxidizing microbes.

表 1. 不同地区红树林沉积物中的硫氧化菌类群

Table 1. The sulfur-oxidizing bacteria groups in different mangrove sediments

Study sites	SOB groups	References
Futian mangrove in Shenzhen, China	*Rhabdochromatium*, *Thioalkalivibrio*	[33]
The mangrove in Fujian, China	*Marichromatium*	[34]
The mangrove in Rio de Janeiro, Brazil	*Chromatiaceae*, *Ectothiorhodospiraceae*	[35]
Mangroves in Sao Paulo, Brazil	*Betaproteobacteria*, *Gammaproteobacteria*	[36]

(*Chromatiales*)中的着色菌科(*Chromatiaceae*)和外硫红螺旋菌科(*Ectothiorhodospiraceae*) 2 种SOB[35]；Maryeimy 等[36]在巴西被石油和城市垃圾污染的红树林中发现存在丰富的 β-变形菌纲和 γ-变形菌纲的 SOB。综上所述，在红树林沉积物中，硫氧化功能菌以变形菌为优势类群，环境的复杂性会增加 SOB 多样性。

用于跟踪硫循环相关的生物分子标记主要是基于编码关键酶的功能基因。目前，硫氧化途径的关键功能基因包括 *sqr* (编码硫醌氧化还原酶)、*soxB* (编码硫氧化酶)[37]和 *dsrA* (编码反向异化硫酸盐还原酶)。在珠江流域的研究中，定量分析显示具有 *soxB* 功能基因的 SOB 比具有 *sqr* 和 *dsrA* 功能基因的 SOB 更丰富，是硫氧化的主要贡献者[31]。在具有 *sqr* 功能基因的 SOB 群落中，披毛菌属(*Gallionella*)、噬氢菌属(*Hydrogenophaga*)、*Limnohabitans*、甲基单胞菌属(*Methylomonas*)、硝化螺菌属(*Nitrospira*)、红育菌属(*Rhodoferax*)和硫针菌属(*Sulfuritalea*)为优势属；对于具有 *soxB* 功能基因的 SOB 群落中，β-变形菌纲脱氯菌属(*Dechloromonas*)、*Limnohabitans*、副球菌属(*Paracoccus*)、硫针菌属和硫杆菌属(*Thiobacillus*)丰度较高；而硫针菌属、硫体属(*Sulfurisoma*)和硫杆菌属在具有 *dsrA* 功能基因的 SOB 群落中数量较多[31]。在红树林生境中，上述 3 种硫氧化途径关键酶编码基因相对应的菌属尚未对比研究，其结果是否一致有待证实。

1.1.2 影响硫氧化过程的主要环境因素：在红树林沉积物中 O_2 浓度、pH、季节、潮汐周期等因素均会影响硫氧化过程[38]。(1) O_2 浓度：SOB 对 O_2 的依赖性不强，除了需氧型的 SOB 外，很多厌氧 SOB 也能在无氧或少氧的条件下进行厌氧氧化。例如，苍白杆菌属(*Ochrobactrum*)以亚硝酸盐(NO_2^-)为电子受体在厌氧的环境下进行硫氧化[39]。(2) pH：SOB 对 pH 的适应性非常广泛，目前已知的 SOB 中性菌、嗜酸菌和嗜碱菌均有报道，但红树林生态系统中的 SOB 多为中性菌。这些 SOB 在不同 pH 条件下利用同一底物时生成的产物会有所差异。例如 $S_2O_3^{2-}$在碱性或者中性条件下被 SOB 氧化成 SO_4^{2-}；而在酸性条件下则被氧化成 $S_4O_6^{2-}$[28]。(3) 季节：沉积物中微生物群落在不同季节有比较大的变化，这些差异性往往是由土壤中可利用养分来决定的。Mishra 等[40]发现，在印度红树林雨季有较高含量的土壤养分，致使雨季比旱季有着更丰富的 SOB。(4) 潮汐周期：在红树林沉积物中，潮汐周期对微生物群落的构成有很大的影响。Zhang 等[41]证实位于红树林潮高滩、潮中滩和海水中的微生物群落有显著差异并且呈现梯度分布。由于潮汐致使红树林的环境条件在时空尺度上发生显著变化，特别是盐度、养分和含氧量，因而影响 SOB 活性。但潮汐周期对 SOB 活性影响程度尚未研究报道。红树林复杂多变的环境极大地丰富了 SOB 多样性，随着测序技术和相关分析手段的飞速发展，新物种有待进一步发掘。

1.2 微生物驱动的硫酸盐还原过程及其影响因素

1.2.1 微生物驱动的硫酸盐还原过程：硫酸盐还原是指在简单有机物降解过程中以 SO_4^{2-}为末端电子受体，最终生成 H_2S 和 CO_2 的还原反应过程[30]。在红树林沉积物与水交界处，硫酸盐还原产生的 CO_2 几乎占据了 CO_2 总排放量的 100%[42]。Kristensen 等[43]在泰国、巴基斯坦、牙买加等地区的红树林沉积物中都检测到了很高的硫酸盐还原活性。硫酸盐还原菌(sulfate-reducing bacteria，SRB)通常被认为是严格厌氧菌[44]，但研究发现部分 SRB 如脱硫弧菌属(*Desulfovibrio*)可以在微量 O_2 的环境中生存[45]。在红树林沉积物中，O_2 仅存在表层几毫米处[46]，以厌氧为主体的环境给 SRB 的生长代谢提供了有利条件。在厌氧环境中，硫酸盐还原是有机物质降解过程中重要的电子转移过程[47]。红树林中有机物的分解主要由发酵过程和 SRB 驱动的硫酸盐还原过程完成[42]，其中超过 50%的有机物分解由 SRB 承担[48]。其基本过程为复杂的碳水化合物经发酵成简单的有机物，SRB 再进一步利用 SO_4^{2-}作为有机物降解的电子受体，最终产生 H_2S 和 CO_2。SRB 在厌氧环境中还能够降解复杂的底物，如长链芳香烃和石油衍生烃[49]。因红树林高硫酸盐的特性及其厌氧环境，丰富的 SRB 及其很强的代谢能力促进了硫元素的快速循环。

据统计，已知的 SRB 目前有 60 个属的 220 多个种[50]。依其反应底物分为 4 类[51–52]：第一类以氢为硫酸盐还原的反应底物，如脱硫肠状菌属(*Desulfotomaculum*)等；第二类以乙醇、乙酸盐、乳酸盐等较简单的有机物为底物，如脱硫弧菌属、脱硫杆菌属(*Desulfobacter*)、脱硫叶菌属(*Desulfobulbus*)和脱硫单胞菌属(*Desulfomonas*)等；第三类以高级脂肪酸为反应底物，如脱硫线菌属(*Desulfonema*)等；第四类以芳香族化合物为反应底物，如脱硫球菌属(*Desulfococcus*)和脱硫八叠球菌属(*Desulfosarcina*)等。红树林沉积物中缺氧和低氧化还原电位的环境特征为硫酸盐还原提供了有利的条件[53]。Quillet 等[54]在英国 Medway 河口的盐沼中发现脱硫弧菌科(*Desulfovibrionaceae*)、脱硫杆菌科(*Desulfobacteraceae*)、脱硫球茎菌科(*Desulfobulbaceae*)、互营杆菌科(*Syntrophobacteraceae*)的存在。在巴西红树林沉积物中存在丰富的脱硫杆菌目(*Desulfobacterales*)、脱硫弧菌目(*Desulfovibrionales*)以及拟杆菌门(*Bacteroidetes*)参与硫还原代谢[36,55]。Ding 等[56]在中国海南红树林中分离培养出芽孢杆菌属(*Bacillus*)、弧菌属(*Vibrio*)、梭状芽胞杆菌属(*Clostridium*)、伯克霍尔德菌属(*Burkholderia*)、希瓦氏菌属(*Shewanella*)和海杆菌属(*Marinobacterium*)的 SRB。Lyimo 等[57]在坦桑尼亚红树林中分离出 1 种脱硫八叠球菌属的 SRB 新菌株 SD1，其可以二甲基硫化物、甲硫醇、丙酮酸和丁酸盐为还原反应的底物。Gomes 等[58]发现在巴西瓜纳巴拉红树林中，2 种常见的红树物种海榄雌属和拉关木选择性地构建脱硫杆菌目和除硫单胞菌目(*Desulfuromonadales*) 2 种 SRB 为根际群落(表 2)。在佛罗里达州，红树林的根际周围，SRB 是细菌群落中丰度最高的一类菌群[59]。综上所述，各种研究表明，因红树林沉积物中蕴含大量的硫酸盐，SRB 成为红树林沉积物中的一大优势类群。

硫酸盐还原途径中的关键基因为 *aprAB* (编码 5′-腺苷酰硫酸还原酶)和 *dsrAB* (编码亚硫酸盐还原酶)[60–62]，*aprAB* 催化 5′-腺苷磷酸硫酸酐转化成腺苷单磷酸盐和 SO_3^{2-}，*dsrAB* 催化 SO_3^{2-}还原成 S^{2-}[36]。现有大量研究通过使用功能基因 *aprAB* 和

表 2. 不同地区红树林沉积物中的硫酸盐还原菌类群

Table 2. The sulfate-reducing bacteria groups in different mangrove sediments

Study sites	SRB groups	References
Salt marsh in Medway estuary, UK	*Desulfovibrionaceae*, *Desulfobacteraceae*, *Desulfobulbaceae*, *Syntrophobacteraceae*	[54]
Mangroves in Sao Paulo, Brazil	*Desulfobacterales*, *Desulfovibrionales*, *Bacteroidetes*	[36,55]
Mangroves in Hainan, China	*Bacillus*, *Vibrio*, *Clostridium*, *Burkholderia*, *Shewanella*, *Marinobacterium*	[56]
Mtoni mangrove in Dar es Salaam, Tanzania	*Desulfosarcina*	[57]
The mangrove in Guanabara Bay, Brazil	*Desulfobacterales*, *Desulfuromonadales*	[58]

dsrAB 作为分子标记来鉴定各种环境中 SRB，例如硫化生物反应器中 SRB 的代谢活性[63]，石油存储库中 SRB 对金属管道的腐蚀[64]等。同样，功能基因鉴定也可以用来推断在红树林沉积物中 SRB 的生态作用。Leloup 等[65]基于 *dsrAB* 功能基因扩增对法国塞纳河河口沉积物中 SRB 的动态特性进行了研究。Bai 等[66]采用高通量功能基因芯片(GeoChip 4.0)分析了中国漳江红树林沉积物中外来入侵物种互花米草相比较本地种有更丰富硫代谢相关微生物群落。目前，利用功能基因标记等分子手段对红树林沉积物中 SRB 的研究较少，揭示红树林沉积物中硫代谢功能相关微生物的生态演变是今后可突破的方向。

1.2.2 影响硫酸盐还原过程的主要环境因素：研究表明，影响 SRB 进行硫酸盐还原过程的几种环境因子分别是有机碳、氧化还原电位、铁离子浓度、O_2 浓度和底物浓度等[67–69]。(1) 有机碳：沉积物中的有机碳是微生物进行硫酸盐还原反应的电子供体，沉积物中 SRB 可代谢的碳源与硫酸盐还原率呈正相关[53]。(2) 氧化还原电位：硫酸盐还原适宜发生于氧化还原电位+100 mv 至–250 mv 范围内[70]。由于硫酸盐还原剂是电子供体的弱势竞争者，它们在竞争中的相对成功主要取决于需氧生物体由于氧耗尽而剩余的碳[71]。因此，SRB 的存在通常指示着氧化还原电位的高低[72]。(3) 铁离子浓度：硫酸盐还原产生的 H_2S 先结合 Fe^{2+}生成 FeS，再结合 S^0 生成 FeS_2。硫化铁是红树林沉积物中硫元素最主要的赋存形式之一[73]。然而，Attri 等[74]实验表明，环境中铁离子浓度也会影响硫酸盐还原活性，过高的铁离子浓度甚至会抑制硫酸盐还原。其中，微生物在铁离子抑制硫酸盐还原反应过程中扮演什么角色有待深入探究。(4) O_2 浓度：红树林沉积物的氧化还原状态会随潮汐周期而波动。在沉积物表层，大部分 SRB 的活性因 O_2 的存在受到抑制；在该氧化区域下，硫酸盐还原通常随深度的增加而增强[75]，直至有机质含量急剧降低的深层，硫酸盐还原开始减弱。Das 等[76]在孟加拉的红树林中发现，SRB 的数量随着沉积物深度的增加而增大，在 60 cm 深度处，SRB 的数量达到最大。(5) 底物浓度：在红树林沉积物的不同深度上，SRB 可利用的各类底物浓度也有差异[77]。深度上不同浓度的底物可以使 SRB 有效地竞争营养物质[78]。SRB 在红树林沉积物中垂直方向上的空间分布是上述各种环境因子综合导致的。

2 微生物驱动硫循环与其他元素循环的耦合

硫循环可以耦合碳、氮、磷和金属元素循环[22,79](图 3)，在红树林沉积物生物地球化学循环中起着举足轻重的作用。SRB 以有机物为电子供

体、以 SO_4^{2-}为末端电子受体进行有机物的矿化作用；其产物 H_2S 被 SOB 利用进行 CO_2 的固定作用[80]。同时，硫酸盐还原过程耦合甲烷(CH_4)厌氧氧化[81–82]，促进碳循环的代谢。此外，硫氧化过程也会耦合硝酸盐还原等氮元素的循环[83]。Griffin 等[84]第一次报道了无氧光养 SOB 利用 NO_2^-作为光合作用的电子供体，将 NO_2^-厌氧氧化成硝酸盐(NO_3^-)；Stevens 等[85]在海洋中富含 NO_3^-的稀氧区发现了 γ-变形菌纲中未培养的硫氧化共生菌。硫循环与金属元素的耦合使 HS^-/S^{2-}与金属离子(如 Zn^{2+}、Cu^{2+}、Hg^{2+}及 Pb^{2+}等)形成金属硫化物沉淀[86–87]，这一耦合能有效地固定沉积物中的重金属[88]。在硫元素接受和释放电子的过程中，Fe(III)被还原成 Fe(Ⅱ)形成 FeS_2，磷溶解释放[18]。在红树林沉积物中，铁、磷和硫元素循环与 SRB 的活性密切相关[89]，铁和磷的可利用性可能取决于 SRB 的活性[90]。Jian 等[91]研究表明，硫酸盐对沉积物中铁和磷元素地球化学循环有显著影响，它显著降低了铁和磷对植物生长的限制，增强了植物对红树林特殊环境的适应力。

在硫酸盐浓度很高的环境中，硫酸盐还原作用会抑制 CH_4 的产生，减少 CH_4 排放，从而对缓解全球变暖具有重要意义。CH_4 对全球的变暖潜能是 CO_2 的 34 倍[92–93]，湿地是 CH_4 最大的自然源。已有研究表明，SRB 与产 CH_4 菌共存于富含硫酸盐的滨海湿地生态系统中并且竞争通用底物[94–96]。由于 SRB 对乙酸盐[97]、氢气[98–99]和甲酸盐[47]等底物具有更高的亲和力，SRB 通常会将这些底物维持在产 CH_4 菌无法利用的较低浓度水平[72]，且硫酸盐还原在热力学上比发酵过程及产 CH_4 过程更有利[100]，硫酸盐还原在富含硫酸盐的环境中比 CH_4 生成更具优势[99,101]。因此，SRB 驱动的硫酸盐还原过程会影响滨海湿地温室气体的排放，并可能进一步影响区域气候。

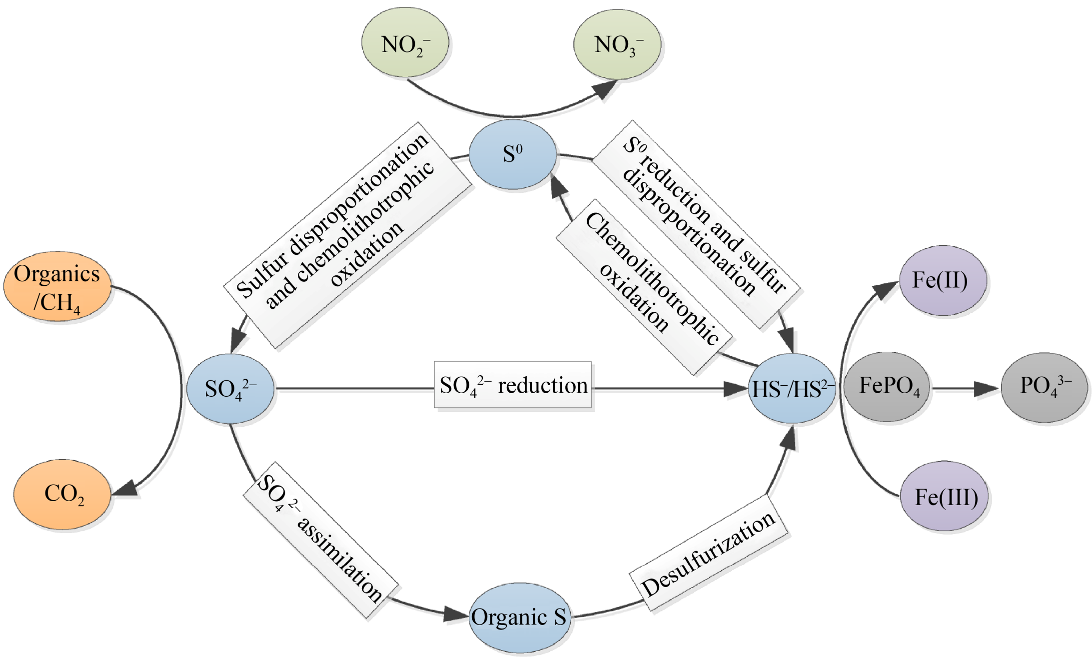

图 3. 硫与其他元素循环的耦合

Figure 3. Coupling processes of sulfur and other element cycles.

3 总结和展望

在红树林沉积物中，SRB 驱动的硫酸盐还原过程相对于 SOB 驱动的硫氧化过程更为活跃，其生物多样性更高，在硫代谢循环中占主导地位。现有的针对红树林硫循环的研究主要集中在可培养微生物，对自然环境条件下驱动硫循环的微生物认识还很有限；SOB 对硫化物解毒起着重要的作用，但其在红树林 O_2 浓度随潮汐多变的环境中的代谢机理仍需进一步研究。因此，将来微生物驱动硫循环的研究应加强如下几个方面：(1) 利用高通量测序技术和基因芯片技术，对具有硫循环功能基因的微生物多样性进行全面分析，探究红树林特殊生态系统中硫代谢特别是硫氧化过程及其关键功能微生物；(2) 通过了解不同深度电子受体及环境因子的分布规律，阐明红树林沉积物中微生物驱动的硫循环与其他生物地球化学元素循环的耦合机制；(3) 结合红树林沉积物中碳、氮、金属元素循环，利用各种组学方法详细探究微生物驱动的硫循环对地球化学大循环的贡献。通过 16S rRNA 基因扩增子测序和鸟枪法宏基因组测序发现，互营杆菌属(*Syntrophobacter*)、硫卵菌属(*Sulfurovum*)、硝化螺菌属(*Nitrospira*)、厌氧绳菌属(*Anaerolinea*)为驱动红树林沉积物中碳、氮、硫循环的主导微生物[102]。这些主导微生物属中都包含硫功能微生物种，对于硫功能微生物耦合各元素循环的具体机制仍需进一步研究。

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Progress in studying microbially-driven sulfur cycling in mangrove sediments

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Abstract: Mangrove forest is a special coastal wetland ecosystem and formed by the periodic mixing of freshwater and seawater. The sediment of mangrove wetland is rich in organic matters, accelerating nutrient cycling driven by resident microbes. Due to high concentrations of sulfate and a variety of sulfide in mangrove sediment, mangrove wetland has been considered as an ideal ecosystem to explore sulfur cycling. This review aims to understand the microbially-driven sulfur cycling, especially sulfur oxidation and sulfate reduction processes in the sediment of mangrove wetland. The major environmental factors affecting sulfur oxidation and sulfate reduction are also discussed. Moreover, future research expectations for microbially-driven sulfur cycling in mangrove ecosystem are indicated.

Keywords: mangrove forest, sediment, microbial community, sulfur oxidation, sulfate reduction, coupling process

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