

# 次生盐化对溪流底栖分解者和凋落物分解的影响

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**摘要:** 次生盐化已经由干旱区的局域环境问题, 蔓延成为全球性生态问题, 严重威胁淡水生态系统生物多样性、生态系统功能和生态系统服务, 然而, 次生盐化对溪流生态系统的效应尚不清晰。以分解者亚系统结构和功能为切入点, 解析次生盐化对溪流分解者群落和凋落物分解过程的影响, 为河溪生态系统保护、管理、修复提供理论依据。在盐化溪流中, 细菌群落和真菌群落对盐化过程的响应模式存在显著差异, 相应作用路径对凋落物分解过程变化的调控能力也不同, 真菌响应更为复杂。盐化可通过致死效应和亚致死效应对底栖动物群落产生显著影响, 撕食者通常对盐度敏感, 盐化作用下底栖撕食者变化对凋落物分解过程的影响非常重要。凋落物分解速率普遍降低, 但凋落物分解过程与水体盐化特征和模式之间的关系尚未确定。后续的研究重点应包括溪流盐化时空动态的生态效应、凋落物分解的元素释放动态等过程参数监测、溪流次生盐化与其他因素(全球变化、富营养化、新兴污染物等)的交互作用等。

**关键词:** 次生盐化; 溪流; 凋落物; 分解; 微生物群落; 底栖动物

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盐度(salinity)是指水体中总的溶解性无机离子盐浓度(Williams & Sherwood, 1994), 淡水盐度通常由 8 种主要离子  $K^+$ 、 $Na^+$ 、 $Ca^{2+}$ 、 $Mg^{2+}$ 、 $Cl^-$ 、 $SO_4^{2-}$ 、 $HCO_3^-$ 、 $CO_3^{2-}$  的浓度决定(Williams, 1987), 常用水体的电导率或总溶解性固体表征(Cañedo-Argüelles et al, 2013; Olson, 2018)。自然状态下淡水生态系统的离子浓度和盐度主要受岩石风化、降水、气溶胶沉降、海水入侵等影响(Gibbs, 1970; Kaushal et al, 2023a), 人类活动导致的淡水生态系统盐度异常升高现象称为次生盐化(secondary salinization; Williams, 2001)。近年, 次生盐化逐渐蔓延、成为全球淡水生态系统可持续发展的主要障碍之一(Cañedo-Argüelles et al, 2016; 2019; Cañedo-Argüelles, 2020; Jeppesen et al, 2020; Cunillera-Montcusí et al, 2022; Kaushal et al, 2023b), 对淡水盐度进行针对性管控是必要且急迫的任务(Bogart et al, 2019; Kaushal et al,

2021; Musie & Gonfa, 2023; Kelly et al, 2024; Soued et al, 2024)。

淡水生态系统中, 流水生态系统生物多样性高(Dudgeon et al, 2006; Ferreira et al, 2023; Agra et al, 2024), 且能为人类提供众多服务功能(Hanna et al, 2018; Lynch et al, 2023)。与大河相比, 低级溪流(low-order stream)拥有庞大的总长度和控制流域面积, 对全流域的生物多样性维持、物质和能量循环、生态系统服务的支撑具有独特而重要的意义(MacDonald & Coe, 2007; Finn et al, 2011; Allan et al, 2021), 但因其规模小、对环境变化敏感, 是世界上受到威胁最严重的生态系统之一(Dudgeon, 2019; Encalada et al, 2019)。目前, 淡水盐化形势日益严峻(Kaushal et al, 2018; 2021; 2023b), 次生盐化已成为溪流生态系统健康的主要威胁之一(丁森等, 2016; Timpano et al, 2018; Martínez et al, 2020a; Mazumder et al, 2021)。

底栖分解者亚系统是溪流生态系统的关键组分, 以陆源凋落物的输入和分解为基础, 支撑高分解者生物多样性和溪流次级生产力(Graça et al, 2015; Brett et al, 2017; Swan et al, 2021), 例如温带森林 70%~90% 的落叶和木质残体输入并维持了溪流和湿地异养食物网(Marcarelli et al, 2011)。Likens & Bormann (1974) 和 Hynes (1975) 最先注意到外源陆生有机物是驱动溪流生态系统中生物群落结构、食物网构建和物质循环的关键资源, 相关主题渐成淡水生态学研究核心问题之一(Van note et al, 1980; Larsen et al, 2016; Boyero et al, 2021;

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Robbins et al, 2023)。底栖分解者亚系统结构与功能完整是溪流生态系统健康的基本保证和指示指标,可作为次生盐化等全球变化因素生态效应研究的理想切入点。

国外关于河溪生态系统次生盐化生态效应的研究较早,案例丰富,我国仅有少量零散案例研究(樊自立等, 2002; 陈小兵等, 2008; Yang et al, 2023; Pang et al, 2024; Zi et al, 2024),张远课题组报道了中国东北浑河-太子河流域采矿引起盐化溪流的系列实验研究(Zhao et al, 2018; Zhao et al, 2020; Zhao et al, 2021)和一篇综述性研究(丁森等, 2016)。次生盐化对溪流生态系统功能和过程的影响是研究的薄弱环节,本研究从溪流分解亚系统结构和功能切入,解析其对溪流分解者群落和分解过程的影响,以期引起国内生态环境学者和管理者对淡水次生盐化问题的关注,为淡水生态学发展和河溪生态系统保护与修复等提供理论依据。

## 1 淡水次生盐化及盐化综合征

地表水体盐化程度根据 Battaglia (1959)的经典划分标准可分为:淡水(含盐量 $\leq 0.5$  g/L)、寡盐水(0.5~4 g/L)、中度盐水(5~18 g/L)、高盐水(>18~30 g/L)、真盐水(>30~40 g/L)、超盐水(>40 g/L)。淡水生态系统的次生盐化问题起初被视为局限于干旱地区的问题(Williams, 2001),干旱区的工农业供水取水、牧场开发和农业垦荒、生产退水等加剧了河流盐化问题(Jolly et al, 2001; Nielsen et al, 2003; Kerr, 2017)。近年研究发现,众多人类活动均可导致淡水次生盐化,主要原因有道路除冰盐的使用(Hintz et al, 2022; Szklarek et al, 2022; Dugan & Arnott, 2023)、采矿等资源开发(Sauer et al, 2016; Vander Vorste et al, 2019; Sowa et al, 2020)、农业活动(Kay et al, 2001; Rengasamy, 2006; Thorslund et al, 2021)、城市化(Moore et al, 2017; Utz et al, 2022; Madge et al, 2024)、生活污水及工业废水排放等(Herbert et al, 2015; Kaushal et al, 2023a)。淡水次生盐化已经超出干旱区的局域问题,成为全球性水生态问题,但现有相关研究主要分布于澳大利亚、北美和欧洲,我国对于地表水次生盐化问题尚无系统研究,亟待开展。

淡水次生盐化导致的系列生态环境、建筑、社会问题统称为淡水盐化综合征(freshwater salinization syndrome, FSS)(Haq et al, 2018; Kaushal et al, 2018; 2019; 2021; 2023b),具体包括:淡水生物多样性下降、水体污染物活化、建筑腐蚀、供水能力受损等。其中,次生盐化对淡水生态系统功能和过程(物质循环、能量流动)影响的研究有限(Berger et al, 2019),需要重点关注。

## 2 溪流底栖分解者亚系统

溪流底栖分解者亚系统(benthic decomposer sub-system)由外源凋落物、底栖动物、微生物及无机环境构成,调控着溪流生态系统的关键功能——凋落物分解过程。该过程可分为非生物过程(淋溶、物理破碎)和生物过程(微生物和底栖动物摄食)(Swan et al, 2021)。微生物是凋落物分解的最大贡献者(Findlay & Arsuuffi, 1989; Hieber & Gessner, 2002),是凋落物和高营养级生物间的能流枢纽(Zhao et al, 2017)。底栖动物也是分解过程的重要贡献者,其作用下的凋落叶损失量可达51%~64%(Hieber & Gessner, 2002)。底栖动物选择性觅食过程也会摄食部分微生物(Arsuffi & Suberkropp, 1989),二者存在复杂的相互作用。

在自然溪流生境中,凋落物的分解速率受到众多非生物和生物因子调控(图1)。凋落物的淋溶和物理破碎主要受凋落物质量(C:N:P、木质素含量、纤维素含量等)、水化学条件(pH、离子浓度等)、水温和流速的影响;微生物和底栖动物对凋落物分解过程的贡献受到生物地理学和系统发育、水流、水温、水化学、底质条件和凋落物质量的影响。溪流次生盐化直接引起溪流水化学条件改变(盐度和离子浓度的增加、pH改变),进而通过直接或间接方式对微生物群落、底栖动物群落产生影响(Vander et al, 2019),最终影响底栖分解者亚系统的结构、功能和过程。

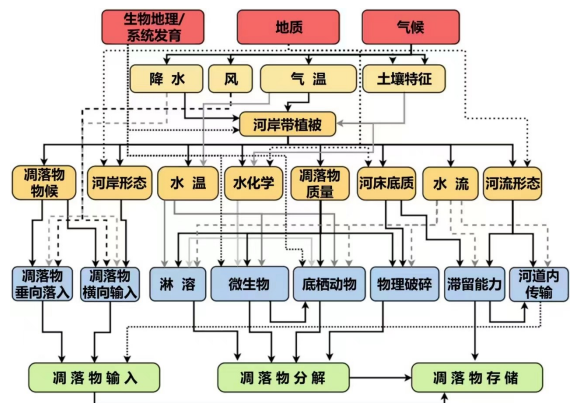


图1 溪流生态系统中凋落物动态驱动因素概念模型

(改编自 Swan et al, 2021)

Fig.1 Conceptual framework outlining the linkages of multiple factors driving litter dynamic (Adapted from Swan et al, 2021)

## 3 次生盐化对溪流底栖分解者的影响

在 Web of Science 数据库中以“stream”(或“river”“freshwater”)、“salinization”(或“salinity”“onic”)和

“decomposition”(或“breakdown”)为关键词,检索得到实验研究论文共 20 篇,包括原位实验 4 篇、实验室微宇宙和中宇宙控制实验 16 篇。实验持续时间从几周到几个月不等,溪流盐化原因包括自然过程(如干旱)和人类活动(采矿、农业退水、道路除冰等)。研究地点主要位于美国、葡萄牙、西班牙和澳大利亚。我们系统分析了 20 篇文献中的微生物(表 1、表 2)、底栖动物(表 3)、凋落物分解速率(表 4、表 5)对溪流次生盐化的响应规律。

### 3.1 次生盐化对微生物的影响

盐度对微生物有 2 种主要的毒性模式:非特异性

的渗透效应和影响特定细胞系统的特异性毒性(Serrano et al, 1999)。淡水盐度变化可引起微生物群落结构改变,对盐度敏感的微生物类群在高盐环境中减少或消失,进而改变群落物种组成和相对丰度。也有研究显示,在中等水平的盐化条件下,一些微生物类群生长状况却可能有所提高,某些真菌在高盐度条件下仍能保持生物活性(Sauer et al, 2016)。通常随着盐度增加,细菌和真菌群落中敏感类群逐渐被耐盐类群取代(Vander Vorste et al, 2019),但二者对盐化的敏感性和耐受能力存在显著差异(图 2)。

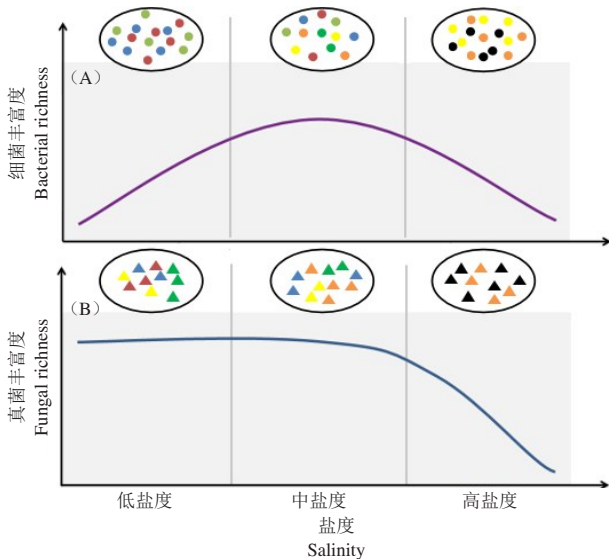
表 1 次生盐化对原位实验凋落物分解过程中微生物的影响

Tab.1 Summary of microbial changes during litter decomposition in field studies related to salinity changes

序号	盐化原因	盐化程度/ $\mu\text{S}\cdot\text{cm}^{-1}$	实验地区	实验持续时间	实验方法	凋落物种类	微生物		离子组成	参考文献	
							总趋势	细菌			真菌
1	干旱	558.1~69 321.5	西班牙	132 d	塑料网架	桦树枝条	微生物活性—	/	生物量 ↓	$\text{Na}^+$ 、 $\text{K}^+$ 、 $\text{Ca}^{2+}$ 、 $\text{Cl}^-$ 、 $\text{SO}_4^{2-}$	Gómez et al, 2016
2	自然	/	西班牙	152 d	凋落物网袋	桉木叶	/	/	生物量和多样性—	/	Jesús et al, 2011
3	采矿	24~1 431	美国	150 d	凋落物网袋	白栎树叶	/	丰富度 ↓	丰富度—	$\text{Na}^+$ 、 $\text{K}^+$ 、 $\text{Ca}^{2+}$ 、 $\text{Mg}^{2+}$ 、 $\text{Cl}^-$ 、 $\text{SO}_4^{2-}$ 、 $\text{HCO}_3^-$	Vander Vorste et al, 2019
4	人为	50~3 500	澳大利亚	7 个月	凋落物网袋	桉树叶	微生物总量↓	/	生物量和多样性 ↓	/	Schäfer et al, 2012

注:测量变量随盐度增加的响应方向:“↓”负相关,“—”没有明确的响应模式。

Note: response direction of measured variables with salinity increase: “↓” negative association, “—” no clear response pattern.



A: 细菌丰富度,不同颜色代表不同种类的细菌;

B: 真菌丰富度,不同颜色代表不同种类的真菌。

图 2 溪流生态系统中微生物物种丰富度随着盐度增加的变化

A: Bacterial richness;

B: Fungal richness. Different colors represent different species.

Fig.2 Changes of microbial species richness as salinity increases in a stream ecosystem

高盐环境会抑制微生物的生长和代谢活动,随着盐度的升高,微生物总量(细菌和真菌)减少,微生

物活性(如呼吸速率和酶活性)降低;此外,盐度还可能影响微生物活动和功能(如产孢率、生长速率和分解能力),进而影响由微生物参与的生态系统过程(Canhoto et al, 2017; Gonçalves, 2019b)。

细菌是淡水凋落物分解的重要参与者(Anesio et al, 2003),盐度是影响细菌群落主要环境因子(Lozupone & Knight et al, 2007),可以直接影响细菌生长状况、活性和个体丰度(Logares et al, 2009; Caporaso et al, 2011)。浮游细菌(Bordalo, 1993; Painchaud et al, 1995; Sleator & Hill, 2002)和附着微生物膜(Zhang et al, 2014; Martínez 2020a; Van Gray et al, 2020)研究均显示,细菌可以适应低盐浓度条件,在高盐浓度下出现高死亡率。细菌物种丰富度与电导率呈显著负相关,随着盐化水平升高而降低,最终全部转变为嗜盐类群(Vander Vorste et al, 2019; Werba et al, 2020)。模拟盐化控制实验检验了盐离子类型对盐化效应的影响,在较高盐度下, $\text{Ca}^{2+}$ 、 $\text{Mg}^{2+}$ 、 $\text{K}^+$ 混合盐处理下的物种丰富度显著高于 $\text{NaCl}$ 单一处理(Devilbiss et al, 2022),这与采矿流域的溪流野外原位监测研究结果存在差异(Bier et al, 2015)。主要原因或为采矿导致溪流次生盐化过程,不仅使盐离子

表2 次生盐化对控制实验凋落物分解过程中微生物的影响

Tab.2 Summary of microbial changes during litter decomposition in controlled studies related to salinity changes

序号	控制盐化方式	盐化程度	实验地区	实验类型	实验持续时间/d	实验方法	凋落物种类	微生物			离子组成	参考文献
								总趋势	细菌	真菌		
1	加入不同浓度的盐	加海盐:0.5、9、13 g/L	美国	实验室中宇宙实验	45	凋落物网袋	红枫、互花米草、芦苇	物种丰富度∩	物种丰富度∩	/	Na <sup>+</sup> 、Cl <sup>-</sup>	Werba et al,2020
2	加入不同浓度的盐	加海盐:0.3、3.5、7、17.5、28 g/L	澳大利亚	实验室微宇宙实验	21	凋落物网袋	黄曲藻	微生物酶活性↓	/	/	/	Roache et al,2006
3	加入不同浓度的盐	电导率:5 000、10 000、15 000 μS/cm	西班牙	实验室中宇宙实验	16	凋落物网袋	黑杨叶	/	/	真菌生物量∩	Na <sup>+</sup> 、Cl <sup>-</sup> 、Mg <sup>2+</sup>	Cañedo-Argüelles et al,2014
4	加入不同浓度的盐	加NaCl: 低:Na <sup>+</sup> 3.0 mg/L, Cl <sup>-</sup> 3.3 mg/L; 中:Na <sup>+</sup> 14 mg/L, Cl <sup>-</sup> 20.3 mg/L; 高:Na <sup>+</sup> 140 mg/L, Cl <sup>-</sup> 214.7 mg/L	美国	实验室微宇宙实验	42	凋落物网袋	甜胶叶	微生物呼吸↓	/	/	Na <sup>+</sup> 、Cl <sup>-</sup>	Tyree et al,2016
5	加入不同浓度的盐	加NaCl:0.8、16 g/L	葡萄牙	实验室微宇宙实验	42	叶片圆盘法	/	最低呼吸速率↓ 微生物耗氧量↓	/	真菌生物量↓ 产孢率↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Pereira da Silva et al, 2021
6	加入不同浓度的盐	加NaCl: 6 g/L	葡萄牙	实验室微宇宙实验	/	叶片圆盘法	白杨叶	/	/	真菌生物量↓ 产孢率—	Na <sup>+</sup> 、Cl <sup>-</sup>	Gonçalves et al, 2019a
7	加入不同浓度的盐	加NaCl:0.2、4.8、16 g/L	葡萄牙	实验室微宇宙实验	35	叶片圆盘法	橡树叶	/	/	生长速率↓ 产孢率↓ 真菌呼吸↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Canhoto et al, 2017
8	加入不同浓度的盐	加NaCl:0.1、3.6 g/L 电导率: 462、2 426、5 954、11 245 μS/cm	葡萄牙	实验室中宇宙实验	28	叶片圆盘法	橡树叶 栗树叶	/	/	真菌生物量—	Na <sup>+</sup> 、Cl <sup>-</sup>	Almeida et al, 2020
9	加入不同浓度的盐	加NaCl、CaCl <sub>2</sub> 、C <sub>2</sub> H <sub>3</sub> KO <sub>3</sub> : 1、3、6 g/L	葡萄牙	实验室微宇宙实验	20	叶片圆盘法	橡树叶	微生物呼吸↓	/	真菌生物量↓	Na <sup>+</sup> 、K <sup>+</sup> 、Ca <sup>2+</sup> 、Cl <sup>-</sup>	Mantínez et al, 2020b
10	加入不同浓度的盐(脉冲&慢性)	加NaCl:1.4、6 g/L	葡萄牙	原位实验+控制实验	/	凋落物网袋	橡树叶	总微生物活性↓	/	脉冲: 丰富度— 慢性: 丰富度↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Canhoto et al, 2022
11	加入不同浓度的盐(脉冲&慢性)	加NaCl:0.4、6 g/L	葡萄牙	原位实验+控制实验	70	凋落物网袋	橡树叶	微生物呼吸↓	/	脉冲: 生物量∩, 产孢率↓ 慢性: 生物量↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Gonçalves et al, 2019
12	模拟采矿和道路除冰盐	电导率: 对照组:(250 ± 0.00)μS/cm, 处理组:(2 700 ± 300)~ (48 100 ± 900) μS/cm	葡萄牙	实验室控制实验	11	凋落物网袋	赤杨叶 橡树叶	/	/	产孢率↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Oliveira et al, 2021
13	模拟农业和道路除冰	电导率: (198.00 ± 32.30)μS/cm	葡萄牙	原位实验+控制实验	14	凋落物网袋	橡树叶	微生物活性—	/	生物量↓	/	Simões et al, 2023
14	旱地和煤矿&人为添加	旱地电导率: 50 ~ 11 000 μS/cm 煤矿区电导率:2 400 μS/cm 人为电导率: 1 000、10 000 μS/cm	澳大利亚	原位实验+控制实验	/	凋落物网袋	赤桉叶	/	/	生物量—	Na <sup>+</sup> 、Cl <sup>-</sup> 、HCO <sub>3</sub> <sup>-</sup>	Sauer et al, 2016
15	盐水倒灌	电导率:280、2 000、3 300、5 500、9 300、15 300 μS/cm	葡萄牙	中宇宙控制实验	63	凋落物网袋	桉木叶	微生物活性↓	/	真菌生物量↓	/	Abelho et al, 2021

注:测量变量随盐度增加的反应方向:“↓”负相关,“↑”正相关,“∩”倒U形,“∪”正U形,“—”没有明确的响应模式。

Note:response direction of measured variables with salinity increase: “↓” negative association, “↑” positive association, “∩” inverted U shape, “∪” U shape, “—” no clear response pattern.

表 3 次生盐化对凋落物分解过程中底栖动物影响

Tab.3 Summary of macroinvertebrate changes during litter decomposition related to salinity changes

序号	盐化原因	盐化程度	实验地区	实验类型	实验持续时间/d	实验方法	凋落物种类	底栖动物变化	离子组成	参考文献
1	自然	/	西班牙	原位实验	152	凋落物网袋	桤木叶	—	/	Jesús et al, 2011
2	采矿	电导率 24~31 $\mu\text{S}/\text{cm}$	美国	原位实验	150	凋落物网袋	白栎树叶	样点河段: 丰富度↓ 凋落叶袋内: 丰富度—	$\text{Ca}^{2+}$ 、 $\text{Na}^{+}$ 、 $\text{Mg}^{2+}$ 、 $\text{K}^{+}$ 、 $\text{SO}_4^{2-}$ 、 $\text{HCO}_3^{-}$ 、 $\text{Cl}^{-}$	Vander Vorste et al, 2019
3	盐水倒灌	电导率: 280、2 000、3 300、5 500、 9 300、15 300 $\mu\text{S}/\text{cm}$	葡萄牙	中宇宙控制实验	63	凋落物网袋	桤木叶	丰度: 总体↓,先U 后∩ 丰富度:U	/	Abelho et al, 2021
4	人为加入不同浓度的盐	加 NaCl: 0、0.1、1、10 g/L	西班牙	实验室微宇宙实验	/	凋落物网袋	榕树叶	生物量↓	$\text{Na}^{+}$ 、 $\text{Cl}^{-}$	García et al, 2024
5	人为加入不同浓度的盐	加 NaCl: 低: $\text{Na}^{+}$ 3.0 mg/L, $\text{Cl}^{-}$ 3.3 mg/L; 中: $\text{Na}^{+}$ 14 mg/L, $\text{Cl}^{-}$ 20.3 mg/L; 高: $\text{Na}^{+}$ 140 mg/L, $\text{Cl}^{-}$ 214.7 mg/L	美国	实验室微宇宙实验	42	凋落物网袋	甜胶叶	生长状况↓ 摄食状况↓	$\text{Na}^{+}$ 、 $\text{Cl}^{-}$	Tyree et al, 2016

注:测量变量随盐度增加的响应方向:“↓”负相关,“∩”倒U形,“U”正U形,“—”没有明确的响应模式。

Note: response direction of measured variables with salinity increase: “↓” negative association, “∩” inverted U shape, “U” U shape, “—” no clear response pattern.

表 4 盐化对溪流凋落物分解速率影响的原位实验研究

Tab.4 Summary of litter decomposition rate related to salinity change in field studies

序号	盐化原因	盐化程度/ $\mu\text{S}\cdot\text{cm}^{-1}$	实验所在地区	实验持续时间	实验方法	凋落物种类	分解速率变化	离子组成	参考文献
1	干旱	558.1~69 321.5	西班牙	132 d	塑料网架	桦树枝条	↓	$\text{Na}^{+}$ 、 $\text{K}^{+}$ 、 $\text{Ca}^{2+}$ 、 $\text{Cl}^{-}$ 、 $\text{SO}_4^{2-}$	Gómez et al, 2016
2	自然	/	西班牙	152 d	凋落物网袋	桤木叶	—	/	Jesús et al, 2011
3	采矿	24~1 431	美国	150 d	凋落物网袋	白栎树叶	—	$\text{Na}^{+}$ 、 $\text{K}^{+}$ 、 $\text{Ca}^{2+}$ 、 $\text{Mg}^{2+}$ 、 $\text{Cl}^{-}$ 、 $\text{SO}_4^{2-}$ 、 $\text{HCO}_3^{-}$	Vander Vorste et al, 2019
4	人为	50~3 500	澳大利亚	7个月	凋落物网袋	桉树叶	↓	/	Schäfer et al, 2012

注:分解速率随盐度增加的响应方向:“↓”负相关,“↑”正相关,“—”没有明确的响应模式。

Note: response direction of decomposition rate with salinity increase: “↓” negative association, “↑” positive association, “—” no clear response pattern.

增加,还会影响水体碱度及重金属离子、微量元素和营养物质浓度,其中任何一因素变化对细菌丰富度的影响都可能强于盐度,因此应增加盐化溪流原位实验研究,以更准确解析盐化过程的实际生态效应。

真菌通常可比细菌产生更广泛的胞外酶(Kirk & Farrell, 1987),是凋落物分解过程中最活跃的分解者(Kominkova et al, 2000),溪流盐化作用可由真菌群落介导显著影响溪流生态系统功能。水生丝状真菌(AHs)是溪流中凋落物与碎食物网消费者间的枢纽(Zhao et al, 2017),AHs利用碎屑作为碳源(Gulis et al, 2003),通过产生菌丝体和胞外酶改变凋落叶特性(Sinsabaugh et al, 2012),在碎屑物质循环、再生产过程中发挥关键作用(Hieber et al, 2002; Canhoto et al, 2023)。相比于细菌群落,AHs对水体盐化有更

强的耐受性和适应性,其可能通过菌丝体渗透液积累和(或)细胞修饰实现耐盐适应。

一方面,溪流盐化的亚致死效应会使AHs功能受损,与凋落物分解相关的真菌响应变量(真菌生物量、呼吸、产孢率、叶质量损失)都受高盐度的显著负影响(Almeida et al, 2020),特别是真菌呼吸作用随盐度增加而下降(Gómez et al, 2016; Sauer et al, 2016; Canhoto et al, 2017; Gonçalves et al, 2019a; 2019b; Martínez et al, 2020b),从而显著影响凋落物分解速率。另一方面,盐化的致死效应能直接导致真菌群落演替(Schäfer et al, 2012; Cañedo-Argüelles et al, 2014; Sauer et al, 2016; Canhoto et al, 2017; Gonçalves et al, 2019a; 2019b),极端高盐度时,真菌群落中仅存单一的高度耐盐物种,群落组成变化将

表5 盐化对凋落物分解速率影响的控制实验研究

Tab.5 Summary of litter decomposition rate related to salinity change in controlled studies

序号	控制盐化方式	盐化程度	实验地区	实验类型	实验持续时间/d	实验方法	凋落物种类	分解速率变化	离子组成	参考文献
1	加入不同浓度的盐	加海盐:0.5、9、13 g/L	美国	实验室 中宇宙实验	45	凋落物网袋	红枫、芦苇、互花米草	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Werba et al, 2020
2	加入不同浓度的盐	加海盐:0.3、5.7、17.5、28 g/L	澳大利亚	实验室 微宇宙实验	21	凋落物网袋	黄曲藻	↓	/	Roache et al, 2006
3	加入不同浓度的盐	电导率:5 000、10 000、15 000 μS/cm	西班牙	实验室 中宇宙实验	16	凋落物网袋	黑杨叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup> 、Mg <sup>2+</sup>	Cañedo et al, 2014
4	加入不同浓度的盐	加NaCl: 0.0.1、1、10 g/L NaCl	西班牙	实验室 微宇宙实验	/	凋落物网袋	榕树叶	总分解速率↓ 微生物介导↑ 底栖介导↓	Na <sup>+</sup> 、Cl <sup>-</sup>	García et al, 2024
5	加入不同浓度的盐	加NaCl: 低:Na <sup>+</sup> 3.0 mg/L, Cl <sup>-</sup> 3.3 mg/L; 中:Na <sup>+</sup> 14 mg/L, Cl <sup>-</sup> 20.3 mg/L; 高:Na <sup>+</sup> 140 mg/L, Cl <sup>-</sup> 214.7 mg/L	美国	实验室 微宇宙实验	42	凋落物网袋	甜胶叶	U	Na <sup>+</sup> 、Cl <sup>-</sup>	Tyree et al, 2016
6	加入不同浓度的盐	加NaCl:0.8、16 g/L	葡萄牙	实验室 微宇宙实验	42	叶片圆盘法	/	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Pereira da Silva et al, 2021
7	加入不同浓度的盐	加NaCl:6 g/L	葡萄牙	实验室 微宇宙实验	/	叶片圆盘法	白杨叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Gonçalves et al, 2018
8	加入不同浓度的盐	加NaCl:0.2、4、8、16 g/L	葡萄牙	实验室 微宇宙实验	35	叶片圆盘法	橡树叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Canhoto et al, 2017
9	加入不同浓度的盐	加NaCl:0.1、3、6 g/L; 电导率:462、2 426、5 954、11 245 μS/cm	葡萄牙	实验室 中宇宙实验	28	叶片圆盘法	橡树叶 栗树叶	∩	Na <sup>+</sup> 、Cl <sup>-</sup>	Almeida et al, 2020
10	加入不同浓度的盐	加NaCl, CaCl <sub>2</sub> , C <sub>2</sub> H <sub>3</sub> KO <sub>2</sub> : 1.3、6 g/L	葡萄牙	实验室 微宇宙实验	20	叶片圆盘法	橡树叶	总分解速率↓ 微生物介导↑	Na <sup>+</sup> 、Cl <sup>-</sup> 、K <sup>+</sup> 、Ca <sup>2+</sup>	Martínez et al, 2020b
11	加入不同浓度的盐(脉冲&慢性)	加NaCl:1.4、6 g/L	葡萄牙	原位实验+ 控制实验	/	凋落物网袋	橡树叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Canhoto et al, 2023
12	加入不同浓度的盐(脉冲&慢性)	加NaCl:0.4、6 g/L	葡萄牙	原位实验+ 控制实验	70	凋落物网袋	橡树叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup>	Gonçalves et al, 2019b
13	模拟采矿和道路除冰影响	电导率: 对照组250 ± 0.00 μS/cm, 处理组(2 700 ± 300)~ (48 100 ± 900) μS/cm	葡萄牙	实验室 控制实验	11	凋落物网袋	赤杨叶 橡树叶	赤杨分解速率↓ 橡树分解速率—	Na <sup>+</sup> 、Cl <sup>-</sup>	Oliveira et al, 2021
14	模拟农业和道路除冰影响	电导率: (198.00 ± 32.30) μS/cm	葡萄牙	原位实验+ 控制实验	14	凋落物网袋	橡树叶	—	/	Simões et al, 2023
15	旱地和煤矿&人为添加	旱地电导率: 50~11 000 μS/cm 煤矿区电导率: 2 400 μS/cm 人为电导率: 1 000、10 000 μS/cm	澳大利亚	原位实验+ 控制实验	/	凋落物网袋	赤桉叶	↓	Na <sup>+</sup> 、Cl <sup>-</sup> 、HCO <sub>3</sub> <sup>-</sup>	Sauer et al, 2016
16	盐水倒灌	电导率:280、2 000、3 300、5 500、9 300、15 300 μS/cm	葡萄牙	中宇宙 控制实验	63	凋落物网袋	桉木叶	∩	/	Abelho et al, 2021

注:分解速率随盐度增加的响应方向:“↓”负相关,“↑”正相关,“∩”倒U形,“U”正U形,“—”没有明确的响应模式。

Note: response direction of decomposition rate with salinity increase: “↓” negative association, “↑” positive association, “∩” inverted U shape, “U” U shape, “—” no clear response pattern.

进一步影响凋落物分解过程。然而,目前真菌多样性对溪流凋落物分解的影响尚不明确:部分研究显示低多样性真菌群落的分解效率较低(Gonçalves et al, 2015),部分研究观察到真菌多样性与叶片分解过程无显著关系(Duan & Kaushal, 2015)。

### 3.2 次生盐化对底栖动物的影响

溪流次生盐化对底栖动物可产生致死和亚致死效应。不同物种耐盐度不同,其致死效应能显著改

变群落组成,如甲壳纲和软体动物最耐盐化,蜉蝣目和襁翅目昆虫则最敏感(Kefford et al, 2012; Szöcs et al, 2012; 2014)。亚致死效应的形式更多样,如导致底栖动物进食率降低、生长延迟、漂移增加等(Blaissius & Merritt, 2002; Benbow & Merritt, 2004; Kefford et al, 2004; Hassell et al, 2006; Clements & Kotlik, 2016),多种功能性状(如卵生、鳃呼吸)也会对溪流盐化显著响应(Szöcs et al, 2014)。底栖动物介导

的凋落物分解率因溪流盐化而降低,如在重复盐脉冲(最大电导率 15 mS/cm)作用下,黑杨叶片分解率较低,这与溪流中 EPT 丰度降低显著相关(Cañedo-Argüelles et al, 2014),但目前尚不能确定底栖动物(撕食者)丰度和种类变化如何影响凋落物分解过程(Berger et al, 2019)。

底栖动物群落对溪流次生盐化有明显的耐受梯度(Cañedo-Argüelles et al, 2013; Clements & Kotlik, 2016),主要与离子胁迫和渗透调节有关(Kefford et al, 2004; Scheibener et al, 2016)。影响水平取决于盐化水平,也受特定离子组成影响,Schulz & Cañedo-Argüelles (2019)阐述了单一离子对淡水底栖动物的毒性。与  $K^+$ 、 $Ca^{2+}$  和  $Mg^{2+}$  等阳离子相比,  $Cl^-$  和  $SO_4^{2-}$  等阴离子影响更显著(Schuler et al, 2019)。例如,在中等氯化物水平下,底栖动物丰富度呈现强烈的非线性下降,氯化物 30~50 mg/L 时, EPT 类群消失(Sundermann et al, 2015),而 EPT 对溪流底栖动物群落多样性维持以及凋落物分解过程具有突出贡献(Wallace & Webster, 1996),可能最终显著影响凋落物分解过程。

#### 4 次生盐化对溪流凋落物分解的影响

分解速率是衡量凋落物分解速度的指标,是凋落物分解研究中最主要的生态参数。在次生盐化对凋落物分解影响的研究中,原位实验(表 4)和实验室控制实验(表 5),均主要使用凋落物网袋法。粗网袋(网目尺寸通常 5~10 mm)允许底栖动物自由出入,细网袋(网目尺寸通常小于 0.5 mm)防止底栖动物进入,仅有微生物参与凋落物分解过程。

次生盐化溪流的污染源(如除冰盐、采矿废物等)常是混合物,包含多种形式的氮和磷、重金属、氯化物等(Fay & Shi, 2012; Kaushal et al, 2018; Gorostiza & Sauri, 2019),可导致溪流水化学条件剧烈变化,影响凋落物分解过程。盐度增加,凋落物的分解速率普遍呈下降趋势(表 4, 表 5)。但部分研究中,凋落物解速率在中等盐度水平时达最高值(A Almeida et al, 2020; Abelho et al, 2021),可能是由于盐化条件下部分微生物介导的凋落物分解速率有所提高所致(Martínez et al, 2020b; García et al, 2024),表明次生盐化对溪流分解者亚系统的影响模式是复杂的。目前,次生盐化溪流中凋落物分解速率与溪流水化学特征间尚未建立明确的定量关系,但凋落物分解过程有望成为评估次生盐化溪流生态系统功能

完整性的有效工具(Chauvet et al, 2016)。

盐化扰动模式对凋落物分解过程也有显著影响。脉冲性盐分扰动通常比慢性盐分暴露危害更小,分解者群落可以有一定的恢复时间(Cañedo-Argüelles et al, 2014; Oliveira et al, 2021),有研究显示脉冲性盐分输入对底栖动物介导的凋落物分解过程影响更大(Findlay & Kelly, 2011),各种盐化模式均会对凋落物分解速率产生消极影响。

在全球变化的背景下,次生盐化可与杀虫剂(Schäfer et al, 2012)、营养盐(Hale & Goffman, 2006; Swan & DePalma, 2012)、极端水文条件(Gonçalves et al, 2019b)、温度(Verberk et al, 2020)等众多因子形成交互效应,共同影响溪流生态系统结构和功能。所有研究都表明,在生态因子交互压力胁迫下凋落物分解速率显著降低。

#### 5 问题与展望

次生盐化已经成为日益严重的全球性淡水生态问题,能在个体、种群、群落和生态系统等各层次产生影响,威胁水生生物及生态系统健康,最终影响生态系统服务功能的维持。近年来,淡水次生盐化问题引起了各国科学家和管理者的重视,但我国的生态系统次生盐化研究主要集中于土壤,对淡水生态系统的关注十分有限。溪流生态学研究,次生盐化对底栖分解者亚系统影响的研究是薄弱环节,特别是盐度对溪流凋落物分解过程影响的研究不足。

(1)未来相关研究应重视溪流次生盐化问题的管理,建立盐化生态效应评估体系,确定安全盐度阈值,以保护水生态系统的健康和完整性。特别要关注次生盐化对溪流分解者亚系统功能(分解、代谢过程)的作用机制,在监测凋落物分解速率基础上,关注分解过程的元素释放动态等过程参数,加强溪流原位分解实验研究,兼顾盐度时空动态效应。

(2)全球变化背景下,应进一步关注盐化和其他生态因子(如土地利用变化、全球变暖、富营养化、新兴污染物等)的交互作用对溪流生态系统的影响,深入解析次生盐化对溪流分解者亚系统结构和功能的影响机制和可能的应对策略。

(3)生态环境主管部门应尽快将盐化相关指标(电导率、总溶解性固体、主要离子浓度等)作为水生态系统监管和评估体系的必备指标,发展更为快速、精确的水体离子浓度检测方法,制定有效的管理策略来减轻次生盐化的不利影响。

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## Effects of Secondary Salinization on Benthic Decomposers and Litter Decomposition in Streams

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**Abstract:** Secondary salinization is a phenomenon of abnormal increase of fresh water salinity that is caused by a multitude of human activities, including the use of road de-icing salt, mining and other forms of resource development, agricultural activities, urbanization, domestic sewage and industrial wastewater discharge, and so forth. Currently, secondary salinization has evolved from a local environmental issue in arid regions to a global ecological concern, posing a significant threat to the biodiversity, ecosystem functions, and ecosystem services of freshwater ecosystems. In this study, we summarized the influence of secondary salinization on the stream decomposer communities and litter decomposition processes based on 20 related literatures from home and abroad, focusing on the structure and function of the decomposer subsystem. The benthic decomposer subsystem is mainly composed of exogenous litter, benthic animals, microorganisms and inorganic environment, which regulates the key function of the stream ecosystem, namely the litter decomposition process. It aimed to provide a theoretical foundation for the protection, management, and restoration of river and stream ecosystems. Results are as follows: (1) The response patterns of bacterial and fungal communities to the salinization process were significantly different, and the contribution of corresponding paths to litter decomposition was also different in salinized streams. The fungal response is more complex. (2) Salinization can significantly affect benthic macroinvertebrates with lethal and sublethal effects. Shredders are typically sensitive to salinity, and the effects of changes in benthic shredders under salinization on the decomposition process of litter are significant. (3) The decomposition rates of litter generally decrease in salinized streams. However, the relationship between the decomposition process of litter and the characteristics and patterns of water salinization has not yet been determined. Future research should prioritize investigating the ecological effects of temporal and spatial dynamics of stream salinization, the monitoring of process parameters such as element release dynamics of litter decomposition, and the potential interaction between stream secondary salinization and other factors such as global change, eutrophication, and emerging pollutants.

**Key words:** secondary salinization; stream; litter; decomposition; microbial community; macroinvertebrate