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水生植物生态学与生态系统功能研究综述:基于梁子湖国家野外站的系统研究*

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摘　要: 水生植物作为淡水生态系统的关键组成部分,在维持生态系统结构、功能和稳定性方面发挥着重要作用。然而,在全球变化背景下,水生植物正面临富营养化、气候变暖、新型污染物及生物入侵等多重胁迫,导致水生植被尤其是沉水植被呈显著衰退趋势。本文基于武汉大学梁子湖湖泊生态系统国家野外科学观测研究站多年系统性研究成果,从个体、种群、群落及生态系统多个尺度,全面综述了水生植物生态学与生态系统功能研究的主要进展。在个体与种群水平上,揭示了水生植物化学计量特征的环境调控机制,阐明了克隆整合与功能性状对异质生境的适应策略;在群落水平上,解析了生物多样性—生产力关系的关键调控因子及种间互作机制;在入侵生态学方面,系统阐明了环境变化与生物互作驱动外来水生植物入侵的机制,评估了外来植物对物质循环、附生生物群落及污染物响应的生态效应;在遗传进化方面,综合运用多组学手段揭示了水生植物的谱系地理格局、局部适应机制及入侵潜力;在生态恢复方面,通过长期原位监测与野外修复实践,验证了沉水植被重建对内源氮磷负荷的控制效果,提出了复合修复技术及生物调控的新思路。这些研究不仅丰富了对水生植物生态适应与生态系统功能关系的理论知识,也为淡水生态系统的保护、修复与可持续管理提供了重要的理论依据和实践指导。
关键词: 水生植物;功能性状;生物入侵;全球变化;生态恢复;梁子湖国家野外站;微塑料;富营养化;化感作用;克隆整合

Aquatic plant ecology and ecosystem functions: A research review based on systematic studies at the Liangzi Lake National Field Station*

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Abstract: As a critical component of freshwater ecosystems, aquatic plants play an essential role in sustaining the structure, function, and stability of ecosystems. However, under global change scenarios, aquatic plants are confronted with multiple stressors, including eutrophication, climate warming, emerging pollutants, and biological invasions, which have led to a significant decline in aquatic vegetation, particularly submerged macrophytes. Based on systematic research findings accumulated over the years from the Liangzi Lake National Field Station for Scientific Observation and Research, Wuhan University, this paper comprehensively reviews the major advances in the ecology of aquatic plants and their ecosystem functions across the individual, population, community, and ecosystem scales. At the individual and population levels, we revealed the environmental regulatory mechanisms of ecological stoichiometry in aquatic plants and elucidated the adaptive strategies of clonal integration and functional traits in response to heterogeneous habitats. At the community level, we analyzed the key regulatory factors governing the relationship between biodiversity and productivity, as well as the mechanisms underlying interspecific interactions. In the field of invasion ecology, we systematically clarified the driving mechanisms of exotic aquatic plant invasions under the combined effects of environmental change and biotic interactions, and evaluated the ecological impacts of exotic plants on material cycling, epiphytic communities, and pollutant responses. In terms of genetic evolution, we comprehensively employed multi-omics approaches to uncover the phylogeographic patterns, local adaptation mechanisms, and invasion potential of aquatic plants. In the context of ecological restoration, long-term in-situ monitoring and restoration practices have verified the effectiveness of submerged vegetation reconstruction in controlling internal

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nitrogen and phosphorus loading, and new insights into combined remediation technologies and biological regulation strategies were proposed. These studies not only deepen the theoretical understanding of the relationship between the ecological adaptation of aquatic plants and ecosystem functions but also provide an important theoretical basis and practical guidance for the conservation, restoration, and sustainable management of freshwater ecosystems.

Keywords: Aquatic plants; functional traits; biological invasion; global change; ecological restoration; Liangzi Lake National Field Station; microplastics; eutrophication; allelopathy; clonal integration

淡水生态系统在全球生物多样性维持、物质循环和生态系统服务供给中发挥着不可替代的作用[1-3]。水生植物是淡水生态系统的重要初级生产者和生境构建者,其群落动态和生态功能直接关系到整个生态系统的健康与稳定。水生植物根据其生活型可划分为沉水植物、挺水植物、浮叶植物和漂浮植物[4]。沉水植物完全生活在水面以下,如菹草(*Potamogeton crispus*)、穗状狐尾藻(*Myriophyllum spicatum*)、苦草(*Vallisneria natans*)、黑藻(*Hydrilla verticillata*)等,是维持清水稳态的关键功能群。挺水植物扎根于沉积物,茎叶伸出水面,如芦苇(*Phragmites australis*)、香蒲(*Typha orientalis*)、菰(*Zizania latifolia*)等,在湖泊滨岸带形成重要的生态过渡带。浮叶植物叶片漂浮于水面,如莲(*Nelumbo nucifera*)、菱(*Trapa bispinosa*)等,既能吸收水中营养盐,又能获取充足光照。漂浮植物自由漂浮于水面,如水鳖(*Hydrocharis dubia*)、凤眼莲(*Eichhornia crassipes*)、大漂(*Pistia stratiotes*)等。这些不同生活型的水生植物通过吸收水体和沉积物中的过量营养物质,抑制浮游植物过度繁殖;通过根系固定沉积物,减少沉积物再悬浮;还能为鱼类、底栖动物和附生生物提供栖息地和食物来源;参与碳、氮、磷等重要元素的生物地球化学循环[5-7],共同维持着生态系统的结构和功能。

目前,受环境变化的影响,水生生态系统正面临前所未有的多重胁迫。全球气候变化、水体富营养化、新型污染物出现以及生物入侵等[8-9],对水生植物生长、繁殖和分布产生显著影响,导致全球范围内的水生植被(特别是沉水植被),呈现出显著衰退趋势。本文基于武汉大学梁子湖湖泊生态系统国家野外科学观测研究站多年在水生植物生态学领域的研究工作,从水生植物资源分配策略与功能性状响应、入侵机制、全球变化适应和生态恢复实践等角度进行了系统梳理和总结,并对未来的研究趋势进行展望。本文的植物分类与命名系统统一以"Flora of China (http://www.iplant.cn/foc/)"为主要参考标准,并据此统一拉丁学名。

1 水生植物生态适应与群落调控机制研究

1.1 水生植物化学计量的环境调控机制

植物体的元素组成(化学计量)既是环境作用的产物,也是植物适应环境的基础。研究发现,环境胁迫会显著影响水生植物元素之间的关系。例如,盐度变化可诱导植物对硫元素的异速积累,甚至打破常规条件下氮与硫之间的相关性[10]。这种调整并非随机,而是受一种内在的"元素网络"调控,植物倾向于维持氮、磷等主要元素的内稳性,而微量元素则表现出更大的可塑性[11]。这种元素层面的动态平衡能力,直接关系到物种在湿地生境中的表现和群落功能的发挥[12]。从全球尺度分析发现,叶片硫元素与氮、磷的耦合关系还受到植物进化历史和生长型的深刻影响[13]。进一步研究发现,湿地植物在多元素分配上存在一套既保守(受进化约束)又灵活(可响应环境)的异速生长法则,用以协调体内多种元素的分配,维持整体的化学计量稳态[14]。对青藏高原地区的调查研究发现,不同生活型的水生植物对水体盐度的生理适应既存在共性,也表现出物种特异性[15]。对中国东北寒冷温带地区 262 个水生植物群落 2162 个样本的系统调查发现,沉水植物的氮、磷含量显著高于挺水植物和浮叶植物,而碳含量则显著低于其他两种生活型水生植物,更倾向于将更多的营养元素分配到光合作用器官[16]。这些研究从元素角度揭示了环境驱动下湿地植物的适应策略。

1.2 不同环境条件下水生植物的克隆整合与功能性状

面对复杂多变的水生环境,植物演化出了多样的生存策略。在克隆植物中,"克隆整合"是关键的资源共享网络。研究发现,沉水植物苦草母株对子株的支持并非无限,而是随子株独立性增强而减弱[17],且在严重胁迫下这种效应可能仅作用于第一代分株[18]。克隆整合不仅能改变植物自身的生长,还能通过根系影响邻株的根际微生物群落,并在不同营养条件下对漂浮植物和沉水植物群落产生差异化影响[19]。此外,底质类型与光照的交互作用影响着克隆沉水植物的觅食行为[20],而土壤养分空间异质性则显著影响克隆湿地植

物的生长表现[21]。

水生植物对环境胁迫的表现因种而异。例如,沉水植物菹草在增温和富营养化协同作用下,其生长和繁殖策略发生适应性调整[22];底栖鱼类的扰动甚至可诱导沉水植物产生跨代可塑性[23]。这些研究从个体到种群水平,揭示了水生植物对异质生境的适应对策。

1.3 水生植物的生物多样性、功能与环境因子的关系

在群落水平上,水生植物的生物多样性—生产力关系受水深等环境背景值调控[24],而群落生产力的高低更多取决于功能性状的均匀度而非物种数量[25]。干扰、营养水平和植物生活型的交互作用共同影响着功能多样性与生产力的关系[26]。在种间互作方面,不同生活型水生植物的资源分配策略在寒温带表现出显著差异[21]。而溶解性无机碳与底质类型共同调控了穗状狐尾藻的性状表现及其分泌物输入[27]。水生植物通过调整自身性状,与沉积物性质共同塑造了微生物群落[28],并通过改善水质影响附生藻类的丰富度[29]。不同沉水植物物种附生细菌的群落结构和功能存在显著差异[30],且这种关系受全球变化因子(如 CO_2 升高、气候梯度)的调控[31-32]。在更高营养级,螺类等底栖动物通过牧食附生藻类,间接促进沉水植物生长[33],而捕食风险介导的行为调控则为湖泊恢复提供了新的生物操纵思路[34]。这些研究表明,水生植物与环境因子间复杂的互作关系影响着生态系统的功能和稳定。

2 外来水生植物入侵生态学研究

2.1 环境变化与生物互作对外来水生植物入侵的影响

对中国 236 个外来水生植物群落 2267 个样方进行系统调查,调查区域覆盖中国东部、中部、南部和西南部,涵盖池塘、湖泊、沟渠、溪流、河流、湿地和水库等多种淡水生态系统类型;调查共记录到 15 种外来水生植物,其中喜旱莲子草(*Alternanthera philoxeroides*)、凤眼莲、大漂和粉绿狐尾藻(*Myriophyllum aquaticum*)是最常见的外来入侵物种[35]。外来植物的生长特点是其成功入侵的重要因素之一,如克隆整合能力促进了凤眼莲的入侵[36]。与此同时,外来水生植物入侵还受到多重环境因素的驱动。例如,富营养化条件下,入侵种凤眼莲通过增加根系分枝复杂度、调整根系拓扑结构来增强养分获取能力,表现出较强的根系可塑性;而本地种水鳖的根系响应则相对保守,结构调整幅度较小[37]。氮添加可显著改变入侵植物喜旱莲子草与本地植物黄花水龙的功能性状差异,为其竞争优势奠定基础[38];同时,营养富集与夜间人工光照的协同效应进一步强化了外来种对本地种的竞争优势[39]。与本地沉水植物黑藻相比,外来种伊乐藻(*Elodea nuttallii*)对短期硫化氢胁迫具有更好的生长和光合性能,表明其生理耐受性更强,在退化生境中可能获得竞争优势[40]。另外,适度水文扰动(低频、中等幅度水位波动)与高营养底质共同促进了外来种粉绿狐尾藻的生长表现,而水深超过 75 cm 后,底质营养无法补偿水深胁迫,成为外来植物生长的限制因子[41]。此外,土壤养分异质性显著促进了克隆入侵植物(如喜旱莲子草、粉绿狐尾藻)的生长表现和种内竞争能力[21,42],而扰动生境中入侵植物的表型可塑性进一步增强其竞争优势[43-44]。本地植物的生长表现与环境胁迫共同塑造了对入侵的抵抗力:本地植物生物量和多样性水平与入侵抵抗呈正相关,但光照受限或营养富集等环境压力会削弱这种抵抗能力[45];具有相似功能性状的高竞争力本地种可有效抑制入侵种生长[46],而本地水生植物群落整体上能够缓冲外来水生植物入侵的严重程度[35]。

2.2 外来水生植物入侵的生态效应

外来植物入侵对水生生态系统产生了多层次、深远的影响。入侵植物喜旱莲子草入侵显著改变了河湖交错带土壤磷循环:与本地植物群落相比,入侵植物会导致土壤无机磷含量增加、有机磷含量降低,磷的生物有效性提高,且这种改变可能不利于后期原生植被恢复[47]。外来与本地水生植物凋落物的分解差异受化学计量特征和生活型共同调控,进而影响养分循环过程[48]。对于沉水植物,由于入侵植物伊乐藻的次生代谢产物含量显著高于本地种轮叶黑藻,其附生藻类群落呈现出更低的生物量、光合活性、丰度和丰富度[49];对于挺水或漂浮植物,入侵植物(如粉绿狐尾藻、凤眼莲、大漂)对附着藻类具有更强的抑制作用,改变了附生生物群落结构[49-50]。此外,外来挺水植物(凤眼莲、粉绿狐尾藻)对水体污染物环丙沙星的耐受性和代谢能力显著优于本地沉水植物(苦草),表明抗生素污染可能加剧外来植物入侵[51]。在升温背景下,不同温度情景与生物防治的交互作用显著影响了入侵水生植物之间的竞争关系[46],而增温与种间竞争的联合作用则

改变了本地种与入侵种在生长资源分配上的权衡[52]。根系性状方面,不同氮供应水平改变外来植物与本地植物群落的根系构型、分泌物及土壤酶活性,进一步影响地下生态过程[53]。

3 水生植物遗传多样性与适应性进化机制研究

综合运用分子标记、系统发育分析、群体基因组学及生态位模型等多学科手段,系统揭示水生植物的遗传多样性、谱系地理格局、适应性进化机制及入侵潜力。在系统发育与分类学方面,研究修订香蒲属(*Typha*)的世界分布格局与系统发育关系[54],并通过分子数据确认黑三棱属杂交种 *Sparganium longifolium* 的起源[55],同时描述内蒙古地区新种 *Ruppia mongolica*[56]。在群体遗传与生物地理学方面,研究揭示中国南方杉叶藻(*Hippuris vulgaris*)的遗传结构与冰期避难所[57],并阐明其环北极分布的谱系地理格局[58];通过比较香蒲属 4 种植物[59]及轮叶狐尾藻(*Myriophyllum verticillatum*)[60]的遗传多样性,发现地理距离与地形共同塑造了种群分化格局;对穗状狐尾藻的研究则揭示地理与环境因素对遗传分化的相对贡献[61],并开发了该物种的微卫星标记[61]。研究人员通过窄叶黑三棱(*Sparganium angustifolium*)的染色体水平基因组组装[62],以及黑三棱属植物 *Sparganium stoloniferum* 的基因组分析,揭示了其克隆繁殖特性、局部适应机制与种群历史动态[63];通过对川蔓藻属植物 *Ruppia sinensis* 的多组学分析,解析其对水体盐度波动的关键调控防御通路[64];基于野生菰(*Z. latifolia*)的群体基因组数据,检测局部适应信号并预测未来气候下的适应风险[65]。此外,结合遗传数据与生态位模型,还预测了黑藻在美洲的高度入侵潜力[66]。这些研究为水生植物资源保护、分类修订及生态适应机制研究提供重要的理论基础。

4 沉水植被恢复对湖泊内源氮磷调控的效果与机制研究

在典型养殖湖泊湖南大通湖和湖北金湖的水体生态修复过程中,通过长期原位监测、定位研究和控制实验,结合不同修复措施,系统研究沉水植被恢复对湖泊内源氮磷负荷的控制效果。研究表明,沉水植被的成功重建能显著改善水体环境,提高透明度和溶解氧浓度,降低上覆水中氮磷营养盐浓度,改变浮游植物群落动态[67-70],同时,沉水植被恢复显著改变沉积物和水体中的微生物群落结构与功能,通过调控氮循环相关功能微生物的丰度和活性,降低沉积物中氮磷负荷[30,71-72]。沉水植物的生长还能有效降低表层沉积物(0~5 cm)中的氮磷负荷,特别是显著削减有机氮、铵态氮、钙结合态磷及铁/铝/锰结合态磷浓度[72-73]。对于典型养殖湖泊,疏浚虽能短期内去除表层沉积物中的钙结合态磷和有机质,但其效果会随时间减弱[74];相比之下,沉水植被恢复能实现更长效的内源磷控制[73]。进一步研究发现,采用疏浚、钝化剂添加与水生植被种植相结合的复合修复技术,对高污染湖区沉积物内源氮磷再生与释放的控制效果优于单一技术[75]。在河湖交错带,植被恢复还能改变沉积物磷形态的时空分布,降低磷释放风险[76]。此外,沉水植被恢复后,沉积物有机碳储量及其驱动因素也发生显著变化[77]。极端天气(强降雨、强风和极端高温)的综合压力和鱼类饲养引发的营养级联效应,可能引发浅水湖泊从以大型植物为主向以藻类为主的转变;同时,需警惕气候变化可能导致的湖泊磷循环状态突变[69]。捕食风险介导的间接效应能显著抑制草鱼的取食活动和泥鳅的扰动行为,从而减轻沉水植物面临的生物胁迫,间接促进其生长,为湖泊恢复提供新的生物调控思路[34]。

5 展望

尽管梁子湖国家野外站的研究已从多个尺度揭示水生植物的生态适应机制与功能调控途径,为淡水生态保护与修复提供重要理论基础,但在全球变化持续加剧的背景下,未来研究仍需重点关注以下方向:(1)加强多因子复合效应的机制解析,聚焦富营养化、气候变暖、新型污染物和生物入侵等多重胁迫的协同或拮抗作用,借助多组学技术揭示水生植物的分子响应机理;(2)强化长期生态效应监测,追踪沉水植被恢复后生态系统功能的稳定性、新型污染物的生物累积效应及入侵植物对土壤理化特征的长期改造效应;(3)深化地下生态过程研究,阐明根系分泌物—根际微生物—沉积物酶活性的耦联机制及其对养分循环的驱动作用;(4)发展跨尺度整合模型,以关联基因、个体、群落与生态系统层面的过程,从而实现对全球变化背景下水生植被演替及生态系统功能响应的预测预警;(5)优化基于自然的修复技术,通过功能群配置、多物种混植和生物操纵等手段提升群落稳定性,并将水生植被恢复纳入流域一体化管理框架,增强湖泊生态系

统对气候变化的韧性。这些研究的系统推进,将有助于研究者更全面地认知水生植物在淡水生态系统中的核心功能,并为全球变化背景下的湖泊保护与修复提供更坚实的科学支撑。

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