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栾兆擎， 闫丹丹， 薛媛媛， 史丹， 徐丹丹， 刘彬， 王立波， 安玉亭

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滨海湿地互花米草入侵的生态水文学机制研究进展

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摘　要:滨海湿地具有重要的生态服务功能和经济价值,互花米草入侵已经对滨海湿地生态系统产生巨大影响。为深入理解滨海湿地生态系统植被演替过程与水盐梯度等环境因子的耦合关系,完善滨海湿地生态水文学的研究内容和方法,为滨海湿地互花米草生态防治以及滨海湿地生态系统的保护和管理提供科学参考,本文针对水文因子和土壤盐分对互花米草的影响及其生理生态响应、水盐梯度下互花米草的空间格局与生物量反演,以及互花米草的生态格局模拟和预测等方面的国内外相关研究进展进行了梳理和展望。主要结论包括:①水盐梯度决定着互花米草的生理生态特征、物种分布和演替格局;②随着遥感技术的不断发展和地理信息系统技术的不断完善,关于群落尺度上互花米草的空间动态研究也越来越趋向于精确化;③群落尺度上的互花米草格局动态及其生态水文驱动机制的量化将成为今后的研究热点;④在对互花米草空间格局进行预测和模拟时,需综合考虑滨海湿地水动力学过程、植物生理学过程、地形生态演化等过程。

关键词:滨海湿地;互花米草;生态水文;入侵

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Research progress on the ecohydrological mechanisms of *Spartina alterniflora* invasion in coastal wetlands

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Abstract: Coastal wetlands have important ecological services and economic value. Invasion by *Spartina alterniflora* has had several adverse effects on these ecosystems. Therefore, it is critical to understand the inherent ecohydrological mechanisms of invasion. This paper reviewed the research on *S. alterniflora* on the following aspects: ① the influences of hydrological gradients and soil salinity on its physiological and ecological features, ② its spatial pattern and biomass distribution under hydrological and salinity gradients, and ③ the modelling of its successional pattern in coastal wetlands. The main conclusions were that the hydrological and salinity gradients determined the physiological and ecological features, the distribution, and successional pattern of *S. alterniflora*. Further, with the developments in remote sensing technology and GIS methods, research on the spatial dynamics of *S. alterniflora* at the community scale would tend to be more precise. Additionally, quantitative studies on the spatial pattern of *S. alterniflora* and the corresponding ecological mechanisms at the community scale would be a key research area. The hydrodynamic processes, biological patterns and geomorphological evolution processes and so on should be considered in the modeling and forecast of the spatial pattern of *S. alterniflora*.

Keywords: coastal wetland; *Spartina alterniflora*; ecohydrological mechanism; invasion

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滨海湿地位于海陆交错带，独特的水文条件和植被土壤特征，使得滨海湿地具有特殊的生态结构和过程，在维持区域乃至全球生态平衡和生物多样性方面具有不可替代的生态环境服务功能[1-2]；同时，作为典型的脆弱生态敏感区，人类活动以及全球环境变化导致滨海湿地面积日趋下降，生态系统功能也逐渐退化[3-4]。相比其他生态系统，受周期性淹水与土壤高盐度的双重胁迫，加上径流输沙淤积或海浪冲蚀的干扰，滨海湿地生态系统植被结构较为简单，极易遭受生物入侵。相关研究表明，互花米草等外来植物的入侵，已经对滨海湿地生态系统的生物多样性和生态功能产生了多方面的威胁[5-6]。

互花米草作为一种全球性入侵种已引起广泛关注[7]。互花米草于20世纪70年代引入我国，由于其强大的适应性和扩散能力，随即开始在滨海地区大肆扩张，目前已占据我国北起辽宁、南至雷州半岛的广大沿海滩涂[7-8]。如江苏省沿海地区自1982年开始引种互花米草后，现已形成了国内面积最大的苏北互花米草盐沼湿地。1988年苏北互花米草盐沼面积仅为2.3 km^2，目前江苏省互花米草面积已急剧扩张至187.1 km^2，占全国海岸带米草总面积的54%；分布岸线长达410 km，约占江苏省海岸长度的47%[9]。

互花米草是典型的滨海湿地植被类型，作为外来物种，互花米草凭借广盐性、耐淹性、耐低氧性和很强的繁殖能力[10-12]，向潮间带较低部位和土著植被群落扩展和入侵[10]，其对我国海岸带的入侵现状及生态效应已成为当前研究热点。众多研究表明，互花米草会改变水动力学过程和沉积过程，进而对滨海湿地土壤形成和营养物质循环产生显著影响；同时，基于自身生理特性和竞争优势，互花米草还会改变入侵地生态环境，最终形成单一优势群落，显著降低生物多样性，导致原有滨海湿地生态系统生态结构和功能受到严重破坏，进而威胁到整个海岸环境与生态[13-16]。鉴于其入侵性和危害性，互花米草已被列入我国16种首批外来入侵物种名单。目前，国内外相关学者和管理部门已经普遍认识到互花米草入侵对生态环境的影响，并开展了大量相关研究[17-18]，主要集中在互花米草生理特性[19-22]、入侵的竞争机制[23-25]、入侵对滨海湿地生物地球化学循环过程的改变[6, 14, 26-33]、入侵对滨海湿地生态系统结构和功能的影响[17, 34-36]，及其生态防治技术[37-39]等方面。

湿地植物群落分布格局的生态水文驱动机制研究，是科学评估全球变化和人类活动背景下水文环境改变对湿地生态系统影响的基础和关键，也是生态水文学这一交叉学科的重点研究领域。植物作为湿地生态系统结构和生态环境功能的核心，是水文及其他环境因子综合作用的产物[40-42]；水文环境的变化，将直接影响湿地植物的生理生态特征，改变其空间分布格局，进而影响湿地生态系统结构、过程及生态环境功能[43-44]。因此，本文针对滨海湿地典型入侵植物互花米草，从生态水文学关注的水文-植被关系及其响应方面，对国内外相关研究进行了梳理和总结。有助于深入理解湿地植物生态与水文机制的耦合关系，完善湿地生态水文学研究理论和研究内容，同时也为我国滨海湿地互花米草的生态防治提供科学依据。

1 水文因子对互花米草的影响及其生理生态响应

水文情势作为湿地生态系统的首要决定因素，是湿地植被结构、物种多样性、生产力和生态演替的首要驱动因子。全球变化和人为活动对湿地的扰动不断加强，水文情势对湿地植被的影响也日益受到关注，特别是关于特定水文情势与优势植被空间格局关系的定量研究亟待进一步深化。对于滨海湿地而言，水文条件常常决定着植物的生长、物种分布和演替格局[45-47]。持续淹水会影响互花米草的生理过程，但后者可通过生理学和形态学方面的响应来适应这种水淹胁迫[48]。试验表明，持续淹水胁迫下，互花米草的株高、根系、地下生物量均受到一定程度的抑制[48]；一定淹没条件下，互花米草株高的增长率会达到最大值，超过此淹没时长，互花米草的增长率将受到显著抑制；同时其叶面积也随淹没时长增加而呈显著减少的趋势[49]。Janousek等[50]通过控制实验发现互花米草生物量和幼苗数量与水淹条件存在显著的线性关系，在高水位水淹条件下，互花米草地下生物量、细根和幼苗数量显著减少[51]，Snedden等[52]通过水淹和盐分控制实验表明，高水位下互花米草地上和地下生物量随高程和持续淹水时间呈指数规律下降。在大尺度上，O′Donnell等[53]利用遥感数据反演了美国佐治亚州滨海湿地互花米草28年的地上生物量动态，并对其驱动因素进行了分析，发现水位、平均海平面和降水量等因素与互花米草地上生物量显著相关。同时，水文条件也影响互花米草的生物量分配，水位升高条件下，互花米草地上生物量、地上分配比均相应增加；而低水位条件显著促进互花米草根系生长[54]。持续干旱将导致水生植物消失，取而代之的是旱生植物；

而持续洪泛过程将导致湿生植物和挺水植物的空间扩展[55]。Magee等[56]研究发现最丰富的物种群落出现在中等水文条件,即使较小的水位变化或波动也足以导致湿地植物优势种群的转变。Smith等[57]通过长达一个生长季的持续淹水实验发现,持续水淹条件下,互花米草的种群密度下降了86%,同时株高也显著降低,实验表明长期的淹水条件可以消除互花米草。地下水位也会对滨海湿地的植被分布产生影响,Thibodeau等[58]对美国南卡罗莱纳州一处盐沼湿地的研究发现,地下水是决定盐沼湿地植被分布的重要因素,不同地区的地下水流向决定了表层土壤的盐分含量,从而决定着植被的分布。Xiao等[59]认为土壤水分是影响潮汐湿地植被分布的重要因素,据此建立了长江三角洲河口湿地的土壤水动态模型,并与互花米草的分布进行耦合分析,表明长江三角洲互花米草的分布很大程度上受土壤水分的影响。Millard等[60]认为地表高程、淹水频率及持续时间和潮汐幅度等水文条件是决定湿地植被群落分布的主要驱动因素。从目前的研究结果来看,由于各研究的尺度差异和研究方法的不同,最终结果仍存在较大差异。尤其是人工控制实验中,实验条件与野外实地环境(如温度、盐分等)显著不同,致使实验结果的不确定性显著增加。基于野外样地的大规模连续监测可获取自然状态下的理想数据,但工作量大,且调查采样工作极易受天气、潮汐等因素影响,如何克服这些不利因素,保障数据的时空连续性和精确性,是今后相关研究需要克服的一个关键问题。

2 土壤盐分对互花米草的影响及其生理生态响应

土壤作为湿地植被的基质,在一定程度上也会影响乃至决定湿地植物的空间格局。土壤因子可以通过控制植物物种的存活率来影响植被分布,尤其在滨海湿地生态系统中,湿地植被的分布,除受水位的影响外,盐分也是决定滨海湿地植被生理生态特征及空间分布的一个非常重要的因素[45-47, 61-62]。海水潮汐作用越强,则土壤的盐度越高,潮汐带来的营养元素也越丰富。因此,一定盐分范围内,盐分含量越高,互花米草长势越好,生物量也越大;超过这个盐分范围后,将对互花米草的生长产生抑制作用[63-64]。Carrion[65]通过移栽控制实验研究高盐分胁迫下互花米草的生理响应也发现类似结果,在1.5%的盐分浓度下,互花米草的嫩芽高度显著高于土壤含盐量为0的对照处理。Hessini等[22]通过控制水分条件实验发现,互花米草在50%田间持水量时仍能保持存活,只不过光合作用、气孔导度等显著下降,通过渗透调节,互花米草展现出较强的弹性调节能力,水分利用率显著增加,表明互花米草可以在干旱环境下生存。Li等[66]利用控制实验研究了水淹和高盐分环境下互花米草的生理响应,发现在两种情况下互花米草均有较高的适应性,在低盐分或中等盐分条件下,互花米草长势良好,高盐分条件下,互花米草通过泌盐现象仍可适应。因此,在未来海平面上升的情况下,我国滨海湿地互花米草仍会进一步扩张。Tang等[67]通过盐分控制实验发现在0~2%的土壤盐分含量范围内,土著种的生长和繁殖能力随着盐分的增加而下降,但入侵种互花米草的生长和繁殖却随着盐分增加而增强,这说明互花米草能在高盐度的光滩上成功扩散。研究还发现,在盐分0.7%左右,本地种生长速率很高,具有明显的竞争优势,此时互花米草无法取代土著种,土著种群落在低盐区相对稳定。但是,随着盐分的增加,互花米草的生长速率开始增大,在盐分高于1.1%时互花米草具有显著的竞争优势。Verrill[68]通过研究发现,与水文条件相比,土壤盐分是驱动滨海湿地植被变化的首要因子。He等[69]对长江三角洲河口地区湿地植物及其环境因子的研究也发现,土壤盐分是控制植被分布的首要因子,其次是高程因素。Moffett等[70]分析了San Francisco湾盐沼湿地中植被格局与水文和土壤因素之间的关系,认为在高程、距潮沟距离、土壤含水量、土壤盐分等要素中,土壤含水量和土壤盐分是决定盐沼湿地植被分布的决定性因子。White[71]通过交互移植实验证明,互花米草群落对于盐分的变化相当敏感,当盐分增高时,互花米草的扩展速度显著加快。Janousek等[72]基于物种数、覆盖度和物种丰富度等生态因子与土壤盐分、粒度、土壤氮和地表高程等环境要素,采用层次划分、分类和物种累积曲线等分析方法,研究了群落结构与环境梯度的相对重要性,研究表明土壤盐分和高程影响大多数植物物种的变化;水文条件、土壤氮含量和土壤黏粒含量通常居于次要地位;局地盐分变化对物种构成有一定影响;水文条件对物种构成及物种丰富度的影响相对较小,研究认为高程和盐分是决定滨海湿地植被群落结构的首要因素。赵欣胜等[73]研究发现对于黄河三角洲滨海湿地植物而言,土壤养分与盐分是决定植被发育演替的主要因素,其中植被演替方向主要受土壤盐分控制,而植物的生长发育主要受土壤养分含量的影响。湿地

植物因其所处生态位不同，对土壤环境因子的需求也不相同，因此，湿地环境因子的变化决定了不同植被的竞争结果。芦苇在淹水较弱和低盐度土壤环境条件下生长较好，而互花米草适宜生长在淹水较强与高盐环境，因此芦苇主要分布在高程较高的滩涂湿地带，而互花米草主要分布在近水中低潮滩带[74]。Snedden等[75]在路易斯安那滨海湿地植物群落类型与河口水文机制之间的关系研究中，采用k-means聚类算法和指示物种分析法分析了植物群落类型及其指示物种，结果发现在物种丰富度和盐分之间存在显著的负相关关系，群落类型CCA分析表明盐分和潮汐水位是植物群落构成的主要驱动因素。尽管大量研究均表明土壤因子与互花米草空间分布存在一定的相关关系，但是相关研究仍不够深入，尤其缺乏对互花米草与土壤盐分空间分异格局的耦合关系的深入探讨。

3 互花米草的空间格局及生物量反演

随着遥感技术的不断发展和地理信息系统（GIS）技术的不断完善，关于互花米草的空间动态研究也越来越趋向于精确化。受潮汐过程影响，互花米草分布区域大多位于潮间带的中上部位[76-77]。自然条件下互花米草的扩张受气候、地貌过程、水文过程、植被类型及种间竞争的影响，表现出明显的带状特征[78]。李屹等[79]利用15期Landsat影像，结合Google Earth影像，采用最大似然分类法提取了福建漳江口红树林国家级自然保护区红树林与互花米草盐沼的近30年历史变化信息，用于研究红树林和互花米草盐沼之间的空间竞争规律。姚红岩等[80]基于互花米草和芦苇不同物候期的光谱特征，提出了一种将二者生长物候差异与其光谱特征相结合，运用实测剖面观测数据确定光谱指标和阈值的综合提取方法，实现了互花米草-芦苇混合交错带的提取，在此基础上揭示了互花米草与芦苇在不同季节的竞争状况，为不同类型植被信息的提取提供了新的思路。周在明等[81]基于SPOT 6影像，利用植被覆盖度和地上生物量估算了互花米草植株高度，该方法是对高空间分辨率光学影像应用研究的重要尝试。低空无人机遥感技术在中小尺度生态监测中具有明显的高精度优势。周在明等[82]基于可见光低空无人机影像数据，构建了土壤调整植被指数V-MSAVI，用于互花米草植被像元信息的提取。LiDAR的发展，为获取更精确的植被空间数据提供了技术保障。Collin等[83]利用LiDAR数据，基于高分辨率数字地形模型和数字表面模型分析，建立了归一化差分雷达植被指数模型NDLVIM，揭示了加拿大魁北克地区滨海湿地互花米草的分布格局，并对其生物量进行了反演。Wang等[84]利用LiDAR数据和高光谱数据，反演了江苏省大丰市滨海湿地互花米草的生物量，研究表明，利用高光谱数据和LiDAR数据融合的方法，可以准确监测滨海湿地互花米草生物量。Millard等[60]根据地表高程、淹水频率及持续时间和潮汐幅度等决定湿地植被群落分布的主要驱动因素，基于LiDAR数据和GIS分析方法，对加拿大Fundy湾滨海湿地恢复区中的优先恢复区域进行了甄选。可以预见，随着上述生态遥感技术和方法的不断发展，对于互花米草时空格局动态的监测将日益趋向精准化和连续化，使得从群落尺度上揭示互花米草的生态格局动态成为可能。

4 互花米草的空间格局动态预测及模拟

综合现有众多湿地植物研究，小尺度上湿地植物种类、数量的研究已相对不是重点，在较大时空尺度上植被群落的演替及其生态水文驱动机制的量化研究将成为今后的研究热点。其中，水文机制变化-植被动态响应的模拟和预测研究已成为当今国际湿地生态水文研究的关键问题[85]。Milzow等[86]基于地下水埋深和植被分布之间的空间耦合关系，建立了地下水-植被分布模拟模型，对气候变化及不同管理情境下的湿地植被空间格局进行了预测。Snedden等[75]基于植物群落与盐分和潮汐水位的关系，采用多分类Logistic回归分析和Akaike信息论准则方法，对路易斯安那滨海湿地盐分和潮汐水位变化下9种植被群落的出现概率进行了预测，研究表明利用盐分和潮汐水位数据，可以对滨海湿地植被群落进行模拟和预测。王聪[87]认为驱动互花米草沼泽景观演变的主要土壤因子为土壤容重、土壤盐度和土壤水分，基于这些要素建立的模拟模型，能够从机理上揭示互花米草的动态。Huang等[88]基于遥感和GIS技术，利用元胞自动机模型，模拟了九段沙河口湿地互花米草的扩张动态，但该模型从机制上而言是基于互花米草扩张空间的历史过程的规律总结，进而利用该规律对其可能的扩张动态进行预测，模型本身并不能反映限制互花米草分布的水文和土壤理化因子的作用，从本质上应属经验模型。Zheng等[89]结合GIS分析方法和有限元胞自动机模型，对崇明东滩互花米草的扩张范围进行了模拟，模型综合考虑了潮汐水位、植被密度、植被分

类以及潮沟等,与传统的元胞自动机模型相比,具有较高的精度,在一定程度上阐明了限制互花米草扩张的机制,但模型未考虑土壤盐分等环境因子,在应用上具有一定的局限性。综合现有相关研究,在对互花米草空间格局进行预测和模拟时,仅考虑一两个限制性环境因子来确定滨海湿地植被的分布是远远不够的,需要将滨海湿地水动力学过程、植物生理学过程、地形演化等过程综合起来,并运用遥感、数学模型,从而建立一个量化的预测模型[17, 90–91]。

5 结论及展望

互花米草入侵已经对我国滨海湿地生态系统造成了巨大影响,研究互花米草入侵的生态水文学机制,有利于从理论上和方法上丰富和完善湿地生态水文学研究;同时研究结果也可为互花米草的生态防治和滨海湿地的可持续管理提供科学参考。综合国内外相关研究进展,结论如下:

(1)水文条件决定互花米草的生理特征、生物量及其分配、物种分布和演替格局。由于各研究的尺度差异和研究方法的不同,研究结果存在较大差异。

(2)盐分是影响和决定互花米草生理生态特征及空间分布的一个非常重要的环境因素,甚至某些条件下会成为滨海湿地植被变化的首要驱动因子,但互花米草分布与土壤盐分空间分异格局的耦合研究仍有待深入。

(3)低空无人机遥感、LiDAR数据、高光谱数据等生态遥感新技术和新方法的发展,使得从群落尺度上揭示互花米草的生态格局动态成为可能。

(4)植被群落的演替及其生态水文驱动机制的量化将成为今后的研究热点,在对互花米草空间格局进行模拟和预测时,需要综合考虑湿地水动力学过程、植物生理学过程、地形生态演化等过程。

综上所述,针对互花米草的入侵机制,尤其在深入揭示互花米草植被群落与水文、土壤等环境因子的量化关系的基础上,从机理方面深入揭示其入侵的内在生态水文驱动机制的报道仍不多见,相关研究亟需进一步加强。在今后的研究中,应结合野外定位观测和室内分析模拟方法,量化互花米草生理生态特征与水文、土壤等环境因子的耦合关系,确定互花米草植被群落分布的关键决定因子,探讨水文和土壤环境因子胁迫下互花米草植被群落的生理生态响应分布格局和演变趋势,进而预测互花米草的格局动态,从而为互花米草的生态防治及滨海湿地管理提供科学依据。

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