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Eco-Environmental
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环境科学

ENVIRONMENTAL SCIENCE

ISSN 0250-3301 CODEN HCKHDV
HUANJING KEXUE

- 主办 中国科学院生态环境研究中心
- 出版 科学出版社



2020

Vol.41 No.6
第41卷 第6期

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三峡消落带适生植物根系活动调控土壤养分与细菌群落多样性特征

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摘要: 植物通过根系分泌修饰根际土壤微环境. 从植物根系-土壤-微生物三者密切关联的根际土壤微环境角度, 研究三峡消落带植被修复重建后根部土壤微生态动态特征, 对于认识和评估消落带退化土壤环境的生态修复工作具有重要意义. 从三峡库区忠县石宝寨汝溪河消落带植被修复示范基地采集人工植被中 4 种优势植物落羽杉 (*Taxodium distichum*)、立柳 (*Salix matsudana*)、狗牙根 (*Cynodon dactylon*) 和牛鞭草 (*Hemarthria altissima*) 的根际与非根际土壤, 探究其根际与非根际土壤的养分含量与酶活性差异, 同时通过高通量测序进行细菌群落多样性分析, 以阐明三峡消落带不同物种逆境胁迫下的生长适应性以及养分利用策略. 结果表明: ①三峡库区消落带 4 种适生植物根系活动导致根际与非根际土壤养分含量产生显著差异, 主要表现为根际土壤有机质、全氮、碱解氮以及有效磷的显著富集, 而钾素在不同物种间的根际效应变化趋势并不一致; ②蔗糖酶、脲酶以及酸性磷酸酶在 4 种适生植物中均表现出正向根际效应 ($R/S > 1$), 但由于不同物种生理特征的差异, 不同物种根系活动对 3 种土壤酶的激活效应存在差异; ③高通量测序结果显示, 库区 4 种适生植物根际与非根际土壤细菌群落多样性特征并无显著差异, 变形菌门、酸杆菌门、绿弯菌门、放线杆菌门、拟杆菌门、浮霉菌门、蓝藻门、厚壁菌门、硝化螺旋菌门、芽孢杆菌门、未知细菌门以及泉古菌门在消落带 4 种适生植物根部土壤环境中相对丰度最大, 对于 4 种适生植物的营养吸收、疾病抵抗以及消落带逆境适应均发挥着重要的作用.

关键词: 土壤养分; 土壤酶; 土壤细菌群落多样性; 适生植物; 消落带; 三峡水库

中图分类号: X172 文献标识码: A 文章编号: 0250-3301(2020)06-2898-10 DOI: 10.13227/j.hjxx.201911214

Root Activities of Re-Vegetated Plant Species Regulate Soil Nutrients and Bacterial Diversity in the Riparian Zone of the Three Gorges Reservoir

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Abstract: Plants modify the soil microenvironment through root exudation. It is important to study the dynamic changes of soil ecosystem from the perspective of root-soil-microbe interactions after vegetation restoration in the riparian zone of the Three Gorges Reservoir (TGR). The rhizosphere and bulk soils of *Cynodon dactylon*, *Hemarthria altissima*, *Taxodium distichum*, and *Salix matsudana* were collected from the vegetation restoration demonstration base of Ruxi River to explore the differences in nutrient contents and enzyme activities between the rhizosphere and bulk soils. At the same time, the diversity of the bacterial community in the rhizosphere and bulk soils was also investigated using the high throughput sequencing method, with the aim to clarify the growth adaptabilities and nutritional utilization strategies within a more precise rhizosphere range. The results showed that ① Suitable plants enhanced the transformation efficiency of rhizosphere nutrients in different ways to improve their adaptability to the soil environment in the TGR. Compared with bulk soil, root activities had significant effects on nutrient contents in the rhizosphere. Among them, SOC, AN, TN, and AP were enriched significantly to a certain degree, while the changes of potassium were not consistent in different plant species. ② In the process of vegetation restoration, the deposition of litter and root secretion indirectly regulated soil enzyme activity. Invertase, urease, and acid phosphatase, all exhibited positive rhizosphere effects ($R/S > 1$) in these four suitable plant species. However, considering the differences in root structure and physiological characteristics between herbaceous and woody plants, the rhizosphere effect of these three enzymes in four plants was different. ③ The results of high-throughput sequencing showed that there was no significant difference in bacterial community diversity between the rhizosphere and bulk soil of four suitable plant species in the TGR. In addition, Proteobacteria, Acidobacteria, Chloroflexi, Actinobacteria, Bacteroidetes, Planctomycetes, Cyanobacteria, Firmicutes, Nitrospirae, Gemmatimonadetes, WS3, and Crenarchaeota were the twelve most abundant bacterial phyla in the rhizosphere and bulk soils, serving the ecological functions of nutrition absorption and disease suppression. Their colonization was found to be beneficial to the stress resistance of plants growing in harsh riparian ecosystems in the TGR.

Key words: soil nutrients; soil enzyme activity; diversity of soil bacterial community; suitable plant species; riparian zone; Three Gorges Reservoir

收稿日期: 2019-11-23; 修订日期: 2019-12-27

基金项目: 重庆市建设科技项目(城科学 2019 第 1-4-2); 重庆市科技兴林首席专家团队项目(TD2019-2); 中央林业改革发展资金科技推广示范项目(渝林科推 2017-12); 国际科技合作专项(2015DFA90900)

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植物体通过根系与土壤直接接触,实现与土壤生态系统的相互作用.在根际环境中,植物通过根系分泌物(如碳水化合物、氨基酸、有机酸、维生素和脂肪酸等)改变根际土壤理化特性并对根际土壤微生物区系加以修饰与限制^[1].同时,在植物不同生长阶段中也存在根际土壤微生物对植物体的反作用,良好的土壤细菌结构可以改善根际土壤养分状态,提高土壤酶活性,从而促进植物的生长发育^[2].根际土壤微生物作为植物-土壤作用体系的重要组成部分,对植物营养吸收^[3,4]、抗逆性^[5]、土壤有机质分解和养分循环等生态功能发挥重要作用.尤其是在三峡库区消落带,长时间高强度的反季节淹水导致库区消落带土壤严重退化,而植被修复工作能够对这些退化土壤产生良好的生态修复效应,现今已得到广泛推广和实施^[6].在三峡消落带水淹胁迫条件下,植物根际土壤微生物作为反映消落带土壤状况和质量的敏感指标,能够对其生存微环境的变化做出迅速反应,进而影响消落带植物群落并修复其土壤结构与功能^[7].因此,从根际微领域出发探究三峡消落带适生植物根系诱导的土壤特征变化,对库区消落带快速植被恢复技术的开发具有重要意义.

目前,对植物根际土壤微环境的研究广泛涉及多种生态逆境,如冰川^[8]、热带沙漠^[9-11]、重金属严重污染的环境^[12-14]等.相关研究显示,植物根际与非根际微生物菌群具有一定的重叠效应,但每个土壤区室中都有其特有的微生物种类以承担特定的生物功能,且在植物根系调控下,优先定殖的微生物菌群在不同程度上表现出植物生长促进和病原菌抵抗等潜能^[15].土壤生态因子^[16-18](土壤理化性质、土壤酶)以及土壤管理措施^[19](施肥、人工栽种等)对土壤微生物群落的分布格局均具有驱动作用.但在库区消落带特定生境中,适生植物根系活动所引起的土壤微生态变化还知之甚少.因此,本文通过比较研究三峡库区消落带4种适生植物根际与非根际土壤养分含量、土壤酶活性以及土壤细菌群落多样性差异,深入揭示这些适生植物的水淹响应机制,以期为进一步开展三峡消落带植被生态修复工作提供参考依据.

1 材料与方 法

1.1 研究区概况

本研究选取重庆市忠县共和村汝溪河消落带植被修复示范基地(107°32'~108°14'E, 30°03'~30°35'N)为实验研究样地.该区域属于亚热带东南季风区,年积温 5787℃,年均温 18.2℃,无霜期 341

d,日照时数 1 327.5 h,日照率 29%,太阳总辐射能 $3.5 \times 10^5 \text{ J} \cdot \text{cm}^{-2}$,年降水量 1 200 mm,相对湿度 80%,四季分明,雨量充沛,日照充足.该地区为典型的丘陵地貌,坡度 20°~25°,主要的土壤类型为石灰性紫色土,土壤熟化程度较低.由于库区特有的水文变化,消落带内水土流失以及土壤侵蚀较为严重,土壤异质性强^[20].

本研究选取多年生木本植物立柳(*Salix matsudana*)、落羽杉(*Taxodium distichum*)以及多年生草本植物狗牙根(*Cynodon dactylon*)、牛鞭草(*Hemarthria altissima*)为实验材料.本实验所选取的木本与草本植物均为人工栽植于消落带植被修复示范基地中高段海拔区域.其中,木本植物栽植时为大小规格基本一致的两年生实生幼树,行间距为 1 m × 1 m.多年的野外调查结果表明,在历经 6 a 的反复水淹后,4 种适生植物仍表现出良好的生长特性,在消落带出露期迅速恢复生长,快速占据一定空间生态位^[21].采样时 4 种适生植物的基本生长状况见表 1.

表 1 样地内 4 种适生植物基本生长状况(平均值 ± 标准误)

Table 1 Basic growth characteristics of four suitable plant species in the sampling site (mean ± SE, n = 3)

物种	科	株高/cm	胸径/cm
狗牙根(<i>C. dactylon</i>)	禾本科	81.91 ± 2.68	—
牛鞭草(<i>H. altissima</i>)	禾本科	139.08 ± 8.14	—
落羽杉(<i>T. distichum</i>)	杉科	566.67 ± 52.06	5.18 ± 0.54
立柳(<i>S. matsudana</i>)	杨柳科	343.28 ± 36.28	2.71 ± 0.57

1.2 采样方法

于 2018 年 7 月 31 日,即消落带植物恢复生长的旺盛期进行样品采集.根据库区消落带样地内 4 种适生植物的生长分布状况,划定 S 形取样带.草本类型下,在 S 形样带内随机设置 3 块 1 m × 1 m 样方,每个样方之间间隔 10 m.然后在每个样方内按梅花形设置 5 个(15 cm × 15 cm × 20 cm)重复取样土块,参考 Riley 的抖落法^[22,23]采集草本根际土壤,同时采用四分法收集非根际土样.木本类型下,在同一海拔区域随机选取 3 株长势较为一致(株高、基径以及冠幅相近)的植株进行破坏性取样.木本根际土样的采集参照完整土块法^[24-27],在清除树木根基周围土壤表面可见的石头和植物残留物后,用平板利铲沿树干东、南、西、北这 4 个方向分别挖掘 4 个土芯剖面(长 20 cm,宽 20 cm,高 20 cm),分离整个土芯,收集根际与非根际土壤.整个野外采集工作中将距离根系 0~4 mm 以内的土壤视为根际土^[24],挑出土壤中混入的根系,4 个方向的土样混合后装入冷冻泡沫箱立即运回实验室用于后续实验指标分

析测定.

1.3 测定方法

根际与非根际土样分为 3 个部分,一部分土样自然风干,研磨过筛,并通过静电法将土壤中的细小根系分离,用于土壤理化性质测定;一部分土样于 4℃ 储藏,用于土壤酶活性测定;另一部分土样在 -80℃ 条件下保存,用于后续土壤细菌 DNA 提取.

1.3.1 土壤养分的测定

土壤 pH 值采用电极电位法测定(1:2.5 土水比浸提液);土壤有机质(soil organic matter, SOC)采用重铬酸钾外加热法测定;土壤全氮(total nitrogen, TN)含量采用元素分析仪(Elementar Vario EL, Germany)测定;用碱解-扩散法测定土壤碱解氮(alkali hydrolyzed nitrogen, AN)含量;土壤全磷(total phosphorus, TP)、速效磷(available phosphorus, AP)含量测定采用钼锑抗比色法;全钾(total potassium, TK)、速效钾(Available potassium, AK)含量的测定采用电感耦合等离子体发射光谱法(ICP-OES, Thermo Fisher iCAP 6300, UK)^[28-30].

1.3.2 土壤酶活性的测定

蔗糖酶活性采用 3,5-二硝基水杨酸比色法测定,以 1 g 土壤 37℃ 恒温培养 24 h 后生成 1 g 的葡萄糖质量(mg)表示;脲酶活性采用苯酚钠比色法测定,以 1 g 土壤于 37℃ 恒温培养 24 h 生成的 NH₃-N 的质量(mg)表示;酸性磷酸酶活性测定采用磷酸苯二钠比色法,以 24 h 后 1 g 土壤中释放出酚的质量(mg)表示.每个样品 3 个重复,并设无基质对照和无土对照^[26, 27].

1.3.3 土壤微生物群落多样性测定

使用强力土壤 DNA 提取试剂盒(MoBio Power Soil Isolation Kit)依照说明书操作步骤进行样本 DNA 提取.通过 1.2% 琼脂糖凝胶电泳对提取物进行浓度鉴定.提取好的 DNA 于 -20℃ 冷冻保存.采用细菌 16S V4-V5 区通用引物,对每个样品进行 3 个重复扩增,同一样品扩增产物进行混合;前端引物 515F (5'-GTGCCAGCMGCCGCGG-3'),后端引物 907R (5'-CCGTCAATTCMTTTRAGTTT-3');对 PCR 产物进行切胶纯化, Qubit 定量后等摩尔混合,用于建立测序文库.

采用 Illumina HiSeq 测序对根系土壤细菌群落多样性进行分析.对测序下机的粗质量序列根据 barcode mismatch = 0 进行样本拆分,采用 FLASH 软件拼接双端序列,同时通过 cutadapt 软件去除序列中前端引物,并根据质量分数 Q20 对序列进行质控,获得高质量序列^[31].之后采用 UPARSE 算法对

高质量序列进行聚类 OTU 并获得代表序列,在聚类过程中以 RDP gold. fa 为模板去除嵌合体序列,采用 RDP classifier 对 OTU 代表序列进行注释^[32].根据每个样本中含有的序列数目,对 OTU 表进行随机抽样,抽样结果用于下游分析.

1.4 数据处理

采用 SPSS 24.0 进行单因素方差分析(Oneway-ANOVA),比较不同物种间根际与非根际土壤各指标的差异;多重比较采用 Duncan 法;F 检验后通过配对样本 t-检验进行根际与非根际之间差异性分析;采用冗余分析讨论土壤因子与土壤优势细菌门相对丰度之间的相关性.用 Origin 8.5 和 Canoco5 绘图.根际效应以根土比 R/S(根际土/非根际土)表示^[29].

2 结果与分析

2.1 不同适生植物根际与非根际土壤化学特性差异

如表 2 所示,狗牙根与牛鞭草根际土壤 pH 值、全氮、碱解氮、有效磷和有机质含量均显著高于两种木本植物(各比较的 $P < 0.05$);然而,两种草本植物根际土壤中全钾含量却显著低于两种木本植物($P < 0.05$).与之相反,狗牙根以及牛鞭草两种草本植物根际土壤速效钾含量与落羽杉和立柳相比分别并无显著差异($P > 0.05$).

4 种适生植物非根际土壤中全氮以及速效钾含量分别均无显著差异,而狗牙根与牛鞭草非根际土壤中 pH 值、碱解氮以及有效磷含量均显著高于落羽杉与立柳.牛鞭草非根际土壤中全磷含量显著高于其余 3 个物种,且其全钾含量与狗牙根以及落羽杉分别均无显著差异,但却显著低于立柳.与此同时,落羽杉非根际土壤中有有机质含量显著低于立柳与狗牙根,而与牛鞭草无显著差异.

4 种适生植物根际与非根际土壤 pH 值和全钾含量分别均未达到显著差异水平,但有机质、全氮、碱解氮和有效磷含量在 4 个物种根际土壤中的含量均显著高于非根际.同时,速效钾在 4 个物种中也均表现出正向根际效应($R/S > 1$),但这种正效应在牛鞭草和落羽杉根部土壤中并未达到显著水平.与此同时,全磷在狗牙根、牛鞭草以及立柳这 3 个物种中均表现出负向根际效应($R/S < 1$).

2.2 不同适生植物根际与非根际土壤酶活性差异

如图 1~3 所示,虽然牛鞭草根际土壤蔗糖酶活性相较于落羽杉和立柳显著偏高($P < 0.05$),但与狗牙根却无显著差异.牛鞭草根际土脲酶活性显著低于狗牙根和立柳,而与落羽杉根际土脲酶活性无显著差异.同时,牛鞭草和狗牙根根际土壤酸性磷酸

表 2 不同适生植物根际与非根际土壤理化特征¹⁾ (平均值 ± 标准误)

Table 2 Soil properties of four suitable plant species in the rhizosphere and bulk soils (mean ± SE, n = 3)

土壤类型	项目	pH 值	全氮(TN) /g·kg ⁻¹	全磷(TP) /g·kg ⁻¹	全钾(TK) /g·kg ⁻¹
狗牙根实生土壤(<i>D. dactylon</i> soil)	根际(R)	7.2 ± 0.3a	1.83 ± 0.06a	0.62 ± 0.15b	17.57 ± 0.47b
	非根际(S)	7.5 ± 0.2A	0.70 ± 0.02A	0.66 ± 0.01B	18.59 ± 0.23AB
	根际效应(R/S)	0.96	2.62**	0.95	0.95
牛鞭草实生土壤(<i>H. altissima</i> soil)	根际(R)	7.1 ± 0.3a	1.27 ± 0.15b	0.88 ± 0.09a	16.69 ± 0.96b
	非根际(S)	7.3 ± 0.1A	0.70 ± 0.10A	0.89 ± 0.09A	17.52 ± 1.20B
	根际效应(R/S)	0.97	1.81**	0.98	0.95
落羽杉实生土壤(<i>T. distichum</i> soil)	根际(R)	6.2 ± 0.1b	0.73 ± 0.06c	0.58 ± 0.02b	19.90 ± 1.03a
	非根际(S)	6.4 ± 0.3B	0.63 ± 0.06A	0.57 ± 0.03B	18.86 ± 0.62AB
	根际效应(R/S)	0.97	1.38*	1.02	1.06
立柳实生土壤(<i>S. matsudana</i> soil)	根际(R)	6.0 ± 0.3b	0.87 ± 0.06c	0.53 ± 0.09b	18.88 ± 0.90a
	非根际(S)	6.2 ± 0.2B	0.67 ± 0.06A	0.55 ± 0.10B	19.70 ± 1.04A
	根际效应(R/S)	0.96	1.3*	0.96	0.96
土壤类型	项目	碱解氮(AN) /mg·kg ⁻¹	有效磷(AP) /mg·kg ⁻¹	速效钾(AK) /mg·kg ⁻¹	有机质(SOC) /g·kg ⁻¹
狗牙根实生土壤(<i>D. dactylon</i> soil)	根际(R)	41.58 ± 4.60a	5.55 ± 1.05a	28.48 ± 2.02ab	6.39 ± 0.91a
	非根际(S)	11.59 ± 1.15A	1.89 ± 0.55A	22.10 ± 2.09A	4.26 ± 0.54A
	根际效应(R/S)	3.59**	2.94**	1.29*	1.5**
牛鞭草实生土壤(<i>H. altissima</i> soil)	根际(R)	39.56 ± 4.62a	5.50 ± 1.71a	24.62 ± 4.67ab	6.15 ± 0.78a
	非根际(S)	11.34 ± 1.46A	2.71 ± 0.61A	20.88 ± 2.25A	3.30 ± 0.87AB
	根际效应(R/S)	3.49**	2.03**	1.18	1.86**
落羽杉实生土壤(<i>T. distichum</i> soil)	根际(R)	12.10 ± 2.73b	1.38 ± 0.41c	22.70 ± 1.09b	4.39 ± 1.49b
	非根际(S)	9.58 ± 0.44B	0.77 ± 0.10B	22.44 ± 0.94A	2.05 ± 0.27B
	根际效应(R/S)	1.26*	1.79**	1.01	2.14**
立柳实生土壤(<i>S. matsudana</i> soil)	根际(R)	19.40 ± 4.63b	1.00 ± 0.19b	29.89 ± 5.13a	5.06 ± 0.25b
	非根际(S)	6.06 ± 0.43B	0.53 ± 0.22B	23.87 ± 0.67A	3.79 ± 0.27A
	根际效应(R/S)	3.2**	1.88**	1.25*	1.48**

1) 不同小写字母表示不同物种根际土之间差异显著($P < 0.05$), 不同大写字母表示不同物种非根际土之间差异显著($P < 0.05$); * 表示同一物种根际与非根际之间差异显著($P < 0.05$), ** 表示同一物种根际与非根际之间差异极显著($P < 0.01$)

酶活性均显著高于两木本植物。

4 个物种非根际蔗糖酶活性均无显著差异. 狗牙根、牛鞭草与落羽杉非根际土壤脲酶活性相互之间也无显著差异, 但均显著低于立柳非根际土壤. 就酸性磷酸酶活性而言, 狗牙根非根际酸性磷酸酶活性显著高于两木本植物, 而与牛鞭草无显著差异.

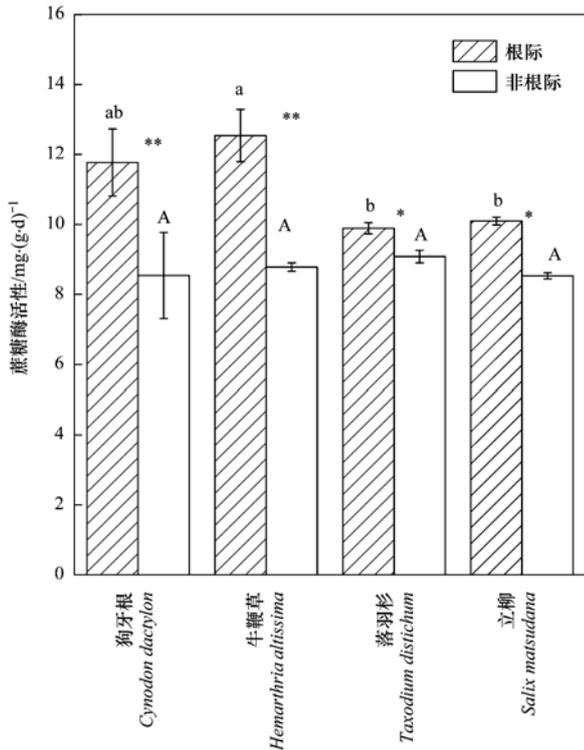
狗牙根、牛鞭草、落羽杉以及立柳这 4 个物种根际土壤蔗糖酶活性均显著大于非根际土 ($P < 0.05$). 狗牙根和立柳根际与非根际土之间脲酶活性的差异分别达到极显著与显著水平 ($P < 0.01$, $P < 0.05$), 而牛鞭草与落羽杉根际中脲酶活性则并未表现出显著差异 ($P > 0.05$). 与此同时, 4 个物种根际与非根际土之间酸性磷酸酶活性的差异分别均达到显著性水平.

2.3 不同适生植物根际与非根际土壤微生物群落多样性

对样本进行聚类注释后, 平均 98.57% 的序列被注释为细菌, 同时 1.43% 的序列被注释为古菌. 在门的水平上, 平均相对丰度大于 1% 的有变形菌

门(Proteobacteria)、酸杆菌门(Acidobacteria)、绿弯菌门(Chloroflexi)、放线杆菌门(Actinobacteria)、拟杆菌门(Bacteroidetes)、浮霉菌门(Planctomycetes)、蓝藻门(Cyanobacteria)、厚壁菌门(Firmicutes)、硝化螺旋菌门(Nitrospirae)、芽孢杆菌门(Gemmatimonadetes)、未知细菌门(WS3)以及泉古菌门(Crenarchaeota), 即样本中的优势菌门除泉古菌门外均为细菌门, 且在狗牙根根际土壤中泉古菌门相对丰度显著高于牛鞭草和立柳 ($P < 0.05$), 而与落羽杉根际土壤中其所占比例无显著差异. 细菌门在 4 个物种根际土壤中所占比例分别均未表现出显著差异 ($P > 0.05$). 另外, 各优势细菌门在 4 种适生植物非根际土壤环境所占比例也均无显著差异 (图 4).

硝化螺旋菌门和泉古菌门在牛鞭草非根际土壤中的相对丰度显著高于根际 ($P < 0.05$), 而变形菌门在牛鞭草非根际土壤中的相对丰度相比根际却显著降低. 泉古菌门与 WS3 分别在落羽杉以及立柳非根际土壤中所占相对丰度显著高于根际, 且芽孢杆



不同小写字母表示不同物种根际土之间差异显著 ($P < 0.05$), 不同大写字母表示不同物种非根际土之间差异显著 ($P < 0.05$); * 表示同一物种根际与非根际之间差异显著 ($P < 0.05$), ** 表示同一物种根际与非根际之间差异极显著 ($P < 0.01$), 下同

图 1 不同物种根际与非根际蔗糖酶活性
Fig. 1 Invertase activities in the rhizosphere and bulk soils of different plant species

菌门在落羽杉以及立柳两种木本植物非根际土壤中相对丰度均高于根际. 然而, 厚壁菌门在狗牙根非根际土壤中的相对丰度显著低于根际.

2.4 4 种适生植物根际与非根际土壤细菌多样性与化学特性之间的相关性分析

冗余分析排序图显示了根际与非根际土壤化学特性与土壤细菌群落组成的相关性. 如图 5 所示, 根际土壤化学特性解释了细菌群落变异性的 40.76%, 且两个排序轴的变异解释度达 67.47%. 酸杆菌门与全氮、碱解氮、速效钾、有效磷、蔗糖酶以及酸性磷酸酶分别呈显著正相关, 而与全磷和全钾呈显著负相关. 浮霉菌门与全磷呈显著正相关. 泉古菌门与 pH 值、脲酶呈显著正相关.

在非根际土壤中, 两个排序轴的变异解释程度高达 86.36%. 且冗余分析结果显示, 变形杆菌门与全氮、速效钾以及脲酶呈显著负相关, 酸杆菌门与全氮、有机质、蔗糖酶呈显著正相关, 而放线菌门与蔗糖酶呈显著负相关. 厚壁菌门与速效钾、全氮以及脲酶均呈显著正相关. 泉古菌门与脲酶、速效钾均呈显著正相关(图 6).

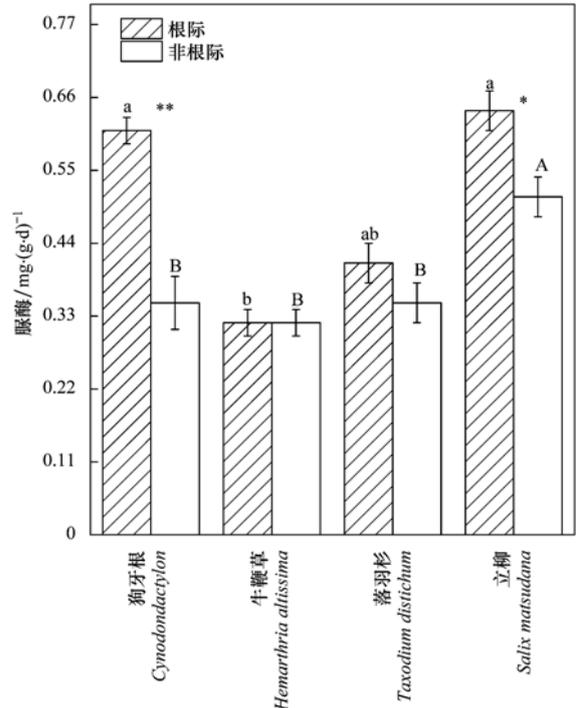


图 2 不同物种根际与非根际脲酶活性
Fig. 2 Urease activities in the rhizosphere and bulk soils of different plant species

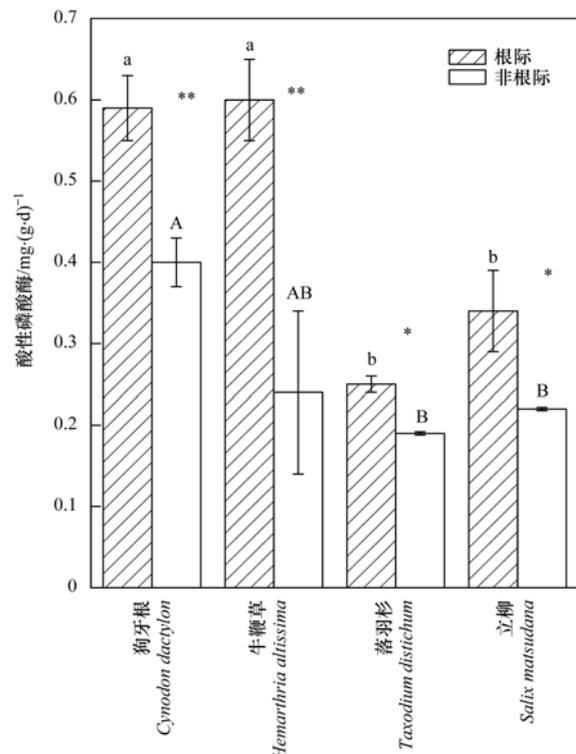


图 3 不同物种根际与非根际酸性磷酸酶活性
Fig. 3 Acid phosphatase activities in the rhizosphere and bulk soils of different plant species

3 讨论

3.1 三峡库区 4 种适生植物根际与非根际土壤化学特性

在养分和环境胁迫时, 植物根系分泌物的成分

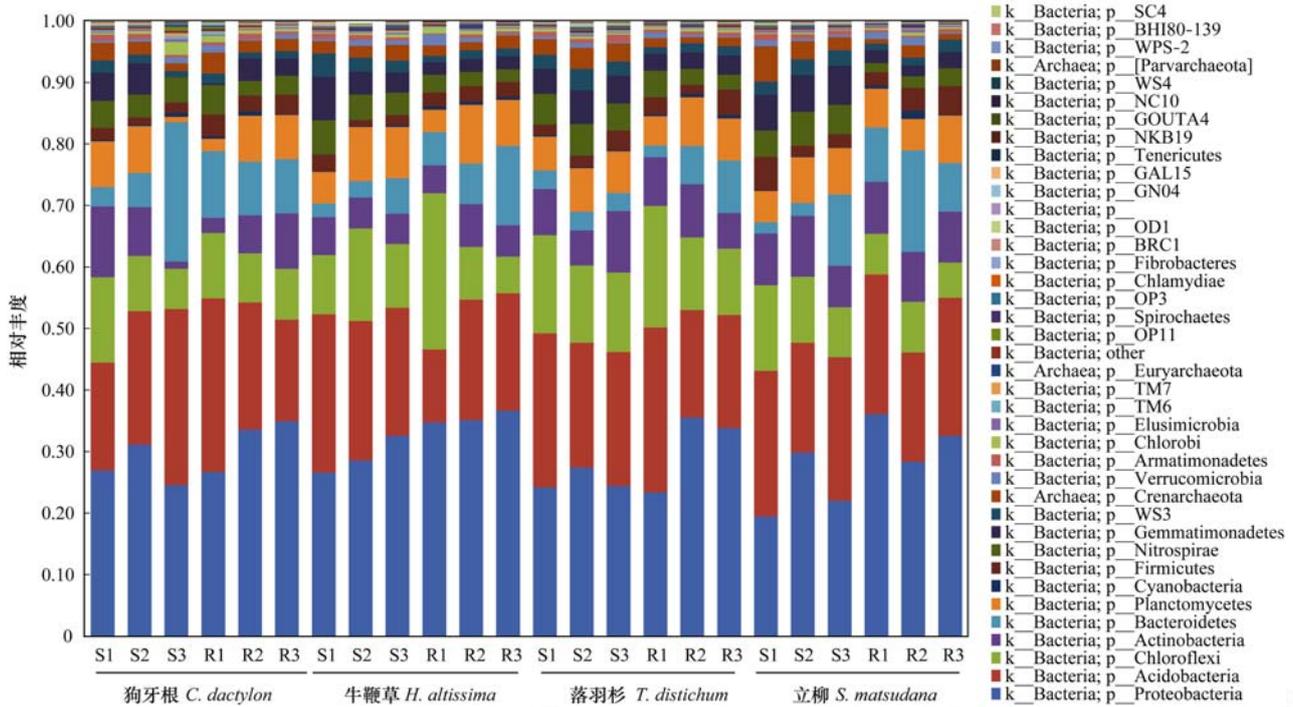


图 4 三峡库区 4 种适生植物根际 (R) 与非根际 (S) 土壤在门水平的细菌群落相对丰度

Fig. 4 Relative abundance (RA) of the bacterial phyla in each soil compartment and plant species

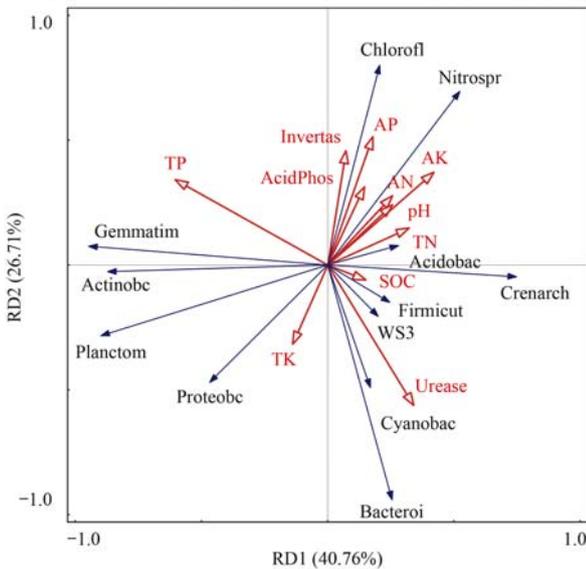


图 5 三峡库区 4 种适生植物根际土壤化学特性与优势细菌群落相关性冗余分析

Fig. 5 Redundancy analysis (RDA) of bacterial communities and soil chemical properties in the rhizosphere

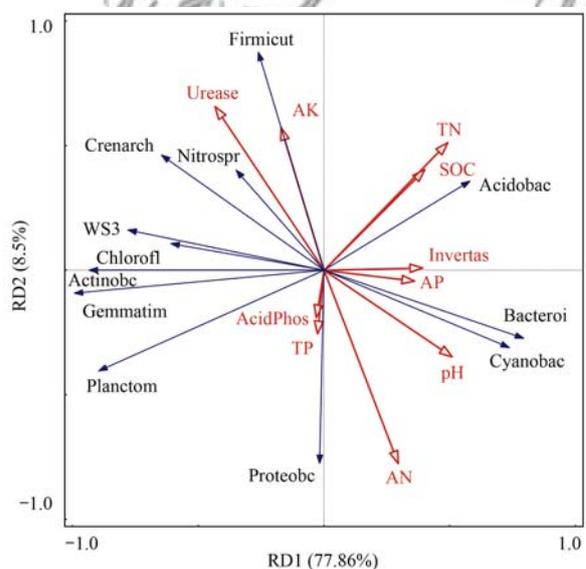


图 6 三峡库区 4 种适生植物非根际土壤化学特性与优势细菌群落相关性冗余分析

Fig. 6 Redundancy analysis (RDA) of bacterial communities and soil chemical properties in the bulk soil

和数量会发生急剧变化以适应环境, 这些植物一般都具有较高的养分利用能力, 因此表现出较强的抗逆性^[33]. 在本研究中, 4 种适生植物根际均发生了有机质、全氮、碱解氮以及有效磷的显著富集, 这在一定程度上说明这 4 种适生植物能够通过积极的生理调节改善其实生土壤养分的生物有效性, 以利于自身的营养吸收. 与此同时, 上述 4 个物种根际与非根际土壤中间各营养元素含量均表现出一定的规律

性. 狗牙根与牛鞭草两种草本植物根际有机质、氮素以及有效磷的含量均显著高于落羽杉与立柳, 这可能是由于植物根系释放碳源促使微生物活性提升并产生大量胞外酶, 进而改变了根际土壤氮和磷的固定和释放平衡. 同时, 植物还可能通过改变分泌有机物的种类影响土壤中微生物的代谢能源, 从而缓解根部土壤中碳、氮和磷化学计量限制^[34-36]. 而 4 种适生植物钾素的根际效应并不一致, 这可能与土壤

含水量、植物物种以及分泌物种类等因素影响土壤中非交换性钾的释放相关^[37]。同时,立柳非根际 TK 含量与落羽杉无显著差异,但其 AK 含量却相对较高,这可能在一定程度上说明立柳根系更强的钾素活化能力,但 7 月时立柳相对落羽杉较为缓慢的生长状况也可能导致其对钾素的消耗较少,从而造成其根际有效钾的相对积累。

前人的研究显示,植物根系所诱导的土壤 pH 值变化决定着根际环境中各矿质营养的生物与化学有效性^[38]。在 7 月,消落带 4 种适生根际土壤均发生不同程度的酸化现象,但这种酸化效应均未达到显著水平。前人研究表明,根际环境中 pH 值的变化与不同植物间遗传特性与代谢机制差异所导致的阴阳离子吸收不平衡有关,乔木的栽植可以使土壤的酸度降低,其具体的原由可能是由根系呼吸分泌 CO₂ 与 H⁺ 所引起的^[16, 39-41],这与本研究中两种木本植物根际与非根际土壤 pH 值均显著低于两草本植物一致(表 2)。另外,尽管两种木本植物根际与非根际土壤的 pH 值均在酸性磷酸酶活性的最适范围内(4.5~6.5),但其供磷水平并没有上升(土壤中有效磷含量显著低于两种草本植物),这极有可能与木本植物较大的个体使得其对磷素的需求与消耗远远大于草本植物有关。

3.2 不同适生植物根际与非根际土壤酶活性差异分析

土壤酶通过影响土壤养分的有效性进而调控植物对养分的吸收与利用。因此,检测土壤酶活性,能够更好地了解土壤中复杂 SOC 的分解以及简单物质的再合成,从而判断土壤肥力的演变趋势^[42]。其中,蔗糖酶是一种重要的转化酶,其活性间接反映了土壤 SOC 积累与分解转化的规律,影响着土壤的熟化程度与肥力状况,是土壤质量评价的重要因子之一^[43]。脲酶与土壤氮素有效性密切相关,其活性常用于表征土壤有机氮的矿化强度。而酸性磷酸酶是植物应对低磷环境以获取有效磷素的重要媒介^[44]。植物根系周围大量的根际沉积使碳和其他能源物质富集,为微生物提供了丰富的营养与能量来源,进而调控土壤酶的释放。因此,本研究中,碳、氮和磷这 3 种循环酶在根际环境中表现出不同程度的激活效应。同时,3 种循环酶活性还受到物种因素的显著影响,这与前人的研究相一致^[45],不同植物代谢及其生物量差异均会通过影响微生物的组成、胞外酶的释放等过程间接调控土壤酶的活性。本研究发现,牛鞭草根际土壤中蔗糖酶与酸性磷酸酶的活性均显著高于立柳,而其根际土壤脲酶的活性却显著低于立柳,在 Stone 等^[9]对土壤营养资源分配理论研究

的基础上,笔者推测可能是牛鞭草根系对复杂氮(如蛋白质等)的分泌导致脲酶活性受到抑制,同时引发了根际土壤微生物一定程度上的碳限制,植物和微生物通过增加蔗糖酶活性来缓解这种限制,同时增强酸性磷酸酶的活性以维持植物与根际微生物对土壤碳、氮、磷营养元素化学计量的需求。

3.3 不同适生植物根际与非根际土壤微生物群落多样性及其影响因素分析

土壤微生物多样性能够较早地反映土壤质量的变化过程,并揭示微生物的生态功能差异,被认为是最有潜力的敏感性生物指标之一^[46]。不同地上植被覆盖改变了阳光与降水对土壤的影响,进而对土壤细菌群落的组成发挥一定的修饰作用^[47]。但在本研究中,4 种适生植物根际与非根际土壤中优势细菌门的相对丰度并无显著差异(图 4),与前人的研究不一致,这极可能与三峡库区特有的水文节律相关。三峡消落带长期水淹导致土壤的匀质化过程加强,土壤高度均质化在一定程度上抵消了物种因素对土壤细菌群落结构的影响。同时,目前大量的研究认为混交林相比纯林具有更为多样的植物输入,因此为更加丰富的细菌群落结构创造了有利条件^[48],而本研究中,各细菌门在 4 个物种根际与非根际土壤中所占比例均未表现出显著差异,这在一定程度上说明在库区周期性水淹条件下,库区适生植物根部土壤环境趋同性较强,从而构建了较为相似的土壤细菌群落结构。

但是,受植物根际沉积的影响,适生植物根际与非根际土壤之间却存在着优势细菌门的显著聚集或离散。泉古菌门在狗牙根根际土壤中的相对丰度显著高于牛鞭草以及立柳。泉古菌门中包含着多种具有固氮功能的细菌种类,前人研究认为泉古菌门与根际土壤中的碳氮含量显著相关,能将无机碳源与氮源转化为细胞能源和有机质^[49],而本研究中狗牙根根际土壤中较高的碳、氮含量,以及泉古菌门与脲酶呈现出显著正相关也进一步验证了这一结论。变形菌门包含多种代谢种类,如与植物共生的细菌(根瘤菌属)以及具有一定降解能力的好氧或兼性细菌^[50, 51]。变形菌门广泛分布于多种生境,通过产生抗生素或其它次生代谢物等途径在抑制病原微生物以及还原难降解有机物中发挥着重要作用^[52, 53]。本研究中,变形菌门在牛鞭草根际环境中所占的比例相比非根际土壤显著升高,这对促进库区植物营养吸收并增强其疾病抵抗能力具有重要作用。厚壁菌门具有一定脱水抗性,能适应干旱等极端环境,并且能有效地抑制土源性疾病^[54]。本研究野外样本采集时正值夏日,长时间的高温环境使得消落带土壤

含水量相对较低,厚壁菌门在狗牙根根际土壤中的显著富集有助于其抵御干旱逆境,实现较好的水分调控.由于脲酶活性对土壤含水量的变化并不灵敏^[55],因此也表现出与厚壁菌门显著的正相关性(图5).

芽孢杆菌门在土壤污染物(如农药、烃等)以及植物凋落物等成分的降解过程中发挥着重要的作用^[56, 57].前人在对香蕉根际土壤的研究中发现,芽孢杆菌门不仅能够促进苗期的植株生长,还能有效地抑制香蕉枯萎病的发生^[58].立柳与落羽杉两种木本植物非根际土壤中的相对丰度较高的芽孢杆菌门有利于库区植物维持相对健康生长的状态.另外,硝化螺旋菌门中包含与氮循环相关的多个菌群(如硝化细菌)^[59],硝化螺旋菌门在牛鞭草非根际土壤中相对聚集有利于库区土壤氮素的相对保存与周转.此外,相关研究显示,pH值对不同酸杆菌类群的影响不完全相同,即不是所有酸杆菌类群都嗜酸^[60].本研究中,根际土壤酸杆菌门与土壤pH值并无显著相关性,这与前人已有的研究结果相一致^[61].本研究中酸杆菌门与土壤中氮、磷、钾的有效性显著相关,这也在一定程度上反映出库区生境中酸杆菌门的营养利用策略.同时有研究表明,酸杆菌门在抑病型土壤中的相对丰度较高^[62],本研究土壤中酸杆菌门为第二大菌门(相对丰度为20.12%),这再次证明了库区消落带植被修复重建之后呈现出较为良好的土壤健康状态.另外,放线菌门作为优势细菌门之一,可有效表征库区消落带适生植物土壤基质的营养有效性.浮霉菌门多数为厌氧菌^[63],本研究中浮霉菌门与速效钾呈显著负相关,这可能与长期厌氧条件增加了土壤中亚铁离子与二价锰离子的浓度,进而与钾离子结合为难溶性的盐,降低土壤中钾离子的有效性有关^[37].

4 结论

(1)消落带不同适生植物根系活动导致碳、氮、磷等养分在根际土壤中发生不同程度的富集,但钾素在不同物种根际与非根际土壤之间的变化并不一致.总体而言,两种草本植物根际实现了更为有效的营养分配与供应.

(2)蔗糖酶、脲酶以及酸性磷酸酶在4种适生植物中均表现出正向根际效应.而由于草本与木本植物不同的根系结构、生理特性等原因,不同物种对于3种土壤酶的激活效应有所差异.

(3)高通量测序结果显示,三峡库区消落带4种适生植物根际与非根际土壤细菌群落多样性特征并无显著差异.变形菌门、酸杆菌门、绿弯菌门、放线

杆菌门、拟杆菌门、浮霉菌门、蓝藻门、厚壁菌门、硝化螺旋菌门、芽孢杆菌门、未知细菌门以及泉古菌门在库区土壤环境中相对丰度最大,对于库区4种适生植物的营养吸收、疾病抵抗以及消落带逆境适应均发挥着重要的作用.

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