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涝害对不同大豆品种根际微生物群落结构特征的影响

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摘要: 淹水影响不同大豆品种根际微生物群落组成, 不同基因型大豆植株耐涝性差异较大。本研究选取耐涝(waterlogging-tolerant, W-T)基因型大豆齐黄 34 和涝害敏感(waterlogging-sensitive, W-S)基因型大豆冀豆 17 为材料, 采用荧光定量 PCR、Illumina MiSeq 高通量测序技术, 分析了不同淹水时间下 2 个基因型根际细菌多样性、群落组成和网络特征。结果表明, 耐涝基因型大豆的生物量和细菌丰度明显高于涝害敏感基因型大豆。主坐标分析(PCoA)表明, 耐涝基因型与敏感基因型大豆微生物群落组成的差异随淹水时间的增加而变化($P < 0.05$)。在淹水条件下, 耐涝基因型大豆富集了 *Yonghaparkia* 属和 *Unclassified-WD2101* 属以及 OTU274 (*Clostridium*)和 OTU2334 (*Desulfosporosinus*)等物种, 这些细菌的富集可能与耐涝性有关, 本研究提供了大豆根际微生物抗涝潜力的证据。

关键词: 大豆; 耐涝; 根际微生物; 16S rRNA; 网络分析

Effects of waterlogging on rhizosphere microorganisms communities of different soybean varieties

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Abstract: Waterlogging affects the composition of rhizosphere microbial community of different soybean varieties. The tolerance of soybean plant with different genotypes to waterlogging is quite different. In this study, waterlogging tolerant soybean genotype (Qihuang 34) and waterlogging sensitive soybean genotype (Jidou 17) were selected. The bacterial diversity, community composition, and network characteristics in the rhizosphere of the two genotypes under different waterlogging time were analyzed via fluorescence quantitative qPCR and Illumina Miseq high-throughput sequencing. The results showed that the biomass of waterlogging tolerant genotype and bacterial abundance in its rhizosphere were significantly higher than those for waterlogging sensitive genotype. The PCoA analysis showed that the difference in microbial community composition between waterlogging tolerant and sensitive soybean genotypes changed with waterlogging time ($P < 0.05$). Under the condition of waterlogging, *Yonghaparkia* and *Unclassified-WD2101*, OTU274 (*Clostridium*) and OTU2334 (*Desulfosporosinus*) enriched in the rhizosphere of the waterlogging tolerant genotype. The enrichment of these bacteria might be related to waterlogging tolerance. This study provides evidence of the microbial potential in the rhizosphere of soybean against waterlogging.

Keywords: soybean; waterlogging tolerance; rhizosphere microorganism; 16S rRNA; network analysis

未来极端气候事件的发生频率将会大幅度增加, 其中包含了干旱、暴雨和随之而来的涝灾^[1-2]。在美国、加拿大、巴西、法国、中国和日本等一些粮食生产关键地区受到极端气候事件的影响尤为显著^[3-5]。

大豆(*Glycine max* L.)是对涝害适应性较差的作物, 当大豆遭受涝害时, 土壤中的氧气含量非常低, 造成了根部呼吸作用减弱进而导致严重的营养供给危机^[6-8]。此外, 涝害胁迫还会干扰作物的生理功能,

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包括叶片光合作用减少、叶、茎和根的气孔封闭以及生长抑制,从而导致产量下降^[9-10]。因此,我们应该尽可能多的理解关于作物耐涝的机制,包括土壤微生物在缓解涝害中的作用^[11-12]。

目前已有多种方法用于提高作物对涝害胁迫的适应能力,包括传统的植物育种、作物的基因工程和植物相关微生物组的管理和应用^[13-14]。作物的植物育种和基因工程可以帮助植物更好地适应胁迫环境^[15]。然而,许多耐胁迫基因型的研究并未考虑土壤环境的生物和非生物因素,特别是微生物对植物的胁迫响应所产生的耐性作用^[16-18]。已有研究表明,根系相关微生物不仅直接受到涝害的影响,同时也间接受到植物对胁迫的响应的影响^[19]。作物受到涝害胁迫,导致地下碳输入数量及质量发生变化^[9,20],进而影响了根际微生物组^[21]。不同植物种类对土壤过程和反馈的特征存在差异,且不同植物基因型在根际会招募不同的微生物组,因此土壤微生物群落在介导植物对涝害胁迫的反应中发挥重要作用^[22-23]。

近年来,越来越多的研究关注于植物微生物组介导的抵抗胁迫研究^[24]。例如,含 1-氨基环丙烷-1-羧酸脱氨酶的有益细菌可以降低胁迫诱导的乙烯含量^[25-26],进而保护植物免受淹水^[27]、干旱^[28]和高盐^[29]等胁迫的有害影响。耐性品种可以通过募集特定的微生物来抵抗外界胁迫^[30-31]。我们基于不同耐铝大豆根际微生物对铝毒的响应机制研究发现,耐铝大豆会招募耐铝的细菌 *Tumebacillus* 和 *Burkholderia*,可以有效帮助耐铝大豆减轻 Al 的毒性^[31]。然而关于大豆涝灾的研究,多数集中关注遗传和栽培措施的改进,而关于不同基因型大豆的根际微生物如何响应涝害的相关研究还未见报道。

基于此,本研究选取耐涝基因型大豆齐黄 34 和涝害敏感基因型大豆冀豆 17 为材料,通过评估不同淹水时长下耐涝和涝害敏感基因型大豆根际细菌多样性及群落结构,来解析涝害程度对不同大豆品种根际微生物的影响差异。本研究强调了根际细菌群落作为潜在育种目标的可能性,以生产对涝害胁迫更耐受的作物。

1 材料与方法

1.1 供试材料

1.1.1 供试土壤 供试土壤为酸性土,采自广东省

英德市(113°42'E, 24°28'N),其包含全碳 10.30 g kg⁻¹、全氮 0.33 g kg⁻¹、全钾 12.15 g kg⁻¹、速效氮 143.5 mg kg⁻¹、速效磷 1.33 mg kg⁻¹、速效钾 115.9 mg kg⁻¹, pH 4.75。

1.1.2 供试大豆 盆栽试验供试大豆(*Glycine max* L.)包括涝害敏感型大豆: W-S (冀豆 17-JD17)^[32];耐涝大豆: W-T (齐黄 34-QH34)^[33]。冀豆 17 由河北省农林科学院粮油作物研究所张孟臣研究员提供,齐黄 34 由山东省农业科学院作物研究所徐冉研究员提供。

1.2 大豆土培盆栽试验

本试验在广东省广州市华南农业大学农学院进行,采用土培盆栽的方式,设置 2 个大豆品种(JD17 和 QH34),1 个无淹水对照,2 个淹水时长处理,共 6 个处理,每个处理设置 6 个重复。2 个淹水时长为 1 d 和 5 d。试验前将风干土壤过 2 mm 的筛,去除杂质备用。采用规格相同的花盆(外径 13.8 cm,内径 13.0 cm,底径 10.4 cm,高 12.2 cm),每盆装风干土约 2.5 kg。在播种前 2~3 d,保持土壤含水量为田间持水量的 50%~60%。播种时,每盆播 8 粒外形一致、壮实饱满的大豆种子,生长过程在可控条件的玻璃房中进行(白天温度为 28~32℃,夜间温度为 16~20℃),出苗 6 d 后定苗至 3 株大豆,出苗期再移至自然光线良好充足的室外继续生长,期间按时管理和除草。生长期间的土壤含水量控制在田间持水量的 80%左右。

播种大豆后待其生长至花期,进行淹水处理。取与种植用花盆等量的相同规格的花盆作为隔水用花盆。将塑料膜裁剪成合适大小的方片,紧贴着隔水用花盆内壁覆盖花盆,用以阻隔水分,防止水分从花盆底下流失,保证淹水处理效果。塑料膜铺好后需要高出花盆 1~2 cm。确认无破孔漏洞后,在种植用花盆外能直接套入外层隔水用花盆,两花盆之间能紧密贴合。添加水量至淹没土壤表面以上 2 cm,每日 2 次定时定量加水,观察并记录生长情况,分别于水淹后 1 d、5 d 时戳破花盆低漏洞处的塑料膜恢复排水,观察并记录。

1.3 土壤样品的收集

不同处理的大豆分别在淹水后 1 d 和 5 d 采用“抖根法”采集根际土壤^[34]。试验总共 6 个处理,每个处理设置 6 个重复,共采集 36 个样品。由于淹水胁迫下,土壤含水量高于最大田间持水量,土壤黏结成块状,实际操作时,需要托起沥去部分水分,轻轻撇掉与大豆根系结合松散的土壤,

然后取下与大豆根系紧密附着的土壤作为根际土壤样品,保存于 -80°C 冰箱。随后将所有土壤样品送深圳华大基因科技服务有限公司,完成土壤微生物总 DNA 的提取、PCR 扩增以及测序数据的初步处理。

1.4 DNA 提取和 qPCR 扩增

利用 Fast kit DNA 试剂盒提取根际土壤总 DNA,提取的 DNA 在去离子水中稀释,并储存于 -20°C 冰箱中保存备用。使用具有 12 nt barcode 引物 338F (5'-ACTCCTACGGGAGGCAGCAG-3')和 806R (5'-GGACTACHVGGGTWTCTAAT-3')扩增 16S rRNA 基因的 V3-V4 高变区^[35]。qPCR 反应体系包括 22.5 μL 的 PCR SuperMix、1.0 μL 正向引物和 1.0 μL 反向引物、10 ng 模板 DNA, ddH₂O 补充至 25 μL 。PCR 扩增体系 95°C 变性 10 min; 95°C 15 s, 60°C 10 s, 72°C 10 s, 28 个循环; 72°C 延伸 10 min^[36]。

1.5 数据分析

使用 QIIME v1.19.1 处理原始序列数据^[37]。删除小于 200 bp 和平均质量分数低于 20 的序列^[38]。通过运行 UCHIME 算法检测潜在的嵌合序列^[39]。用 CD-HIT 按 97%相似性对序列进行 OTU 聚类^[40]。使用 RDP 对数据库执行 OTU 代表序列的分类归属^[41-42]。所有样本均随机重采样至相同序列深度(每个样本 29,169 个序列),以减少测序深度对处理效果的影响。在 QIIME v1.19.1 中计算根际细菌 Alpha-多样性 (Chao1 和 Shannon 指数)。并且基于 Bray-Curtis 距离矩阵进行主坐标分析(PCoA)用于分析不同处理之间微生物群落组成的相似性^[43]。利用非参数多元方差分析(Adonis)计算微生物群落结构的差异。采用 *t* 检验(Student's *t*-test)对相对丰度在前 100 的属进行差异性分析,并利用 Duncan's 法进行多重比较。Venn 分析用于统计不同处理样本中所共有和独有的细菌属的数量。采用 GenStat 统计软件进行大豆生物量、细菌丰度和多样性指数的单因素方差分析(ANOVA),并利用 Duncan's 法来进行多重比较,显著性水平均设为 0.05。

利用共现网络评价相对丰度大于 0.2% 的细菌 OTUs 之间的关系。利用 R 包 psych^[44] 计算 Spearman 相关系数,得到 OTU 之间的成对相关,网络中包含 $r > 0.8$ 和 $P < 0.05$ 的相关。利用 Gephi v.0.9.2 为每个植物基因型和淹水处理构建了共现网络可视化^[45-46]。计算网络的拓扑性质,以阐明不同基因型和淹水处理的群落结构差异。

2 结果与分析

2.1 大豆生物量、根际细菌丰度及多样性

2 种基因型在不淹水和淹水 1 d 处理中生物量无显著差异,在淹水 5 d 时,耐涝基因型大豆生物量显著高于涝害敏感大豆(图 1-a)。淹水降低了大豆根际微生物细菌的基因拷贝数,淹水 5 d 处理中耐涝基因型的细菌基因拷贝数明显高于敏感基因型(图 1-b, $P < 0.05$)。由不同淹水处理根际土壤细菌的多样性指数(图 1-c, d)表明,淹水处理没有对 2 个基因型大豆根际微生物多样性产生影响。

2.2 不同处理根际细菌的群落结构

对 36 个土壤样品测序共获得了 1,304,142 条有效序列,每个样品 19,852~37,180 条,平均 35,603 条,在 97%相似度下聚类得到 5538 个 OTU。在 6 个处理中只检测到 41 个门,其中变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)、绿弯菌门(Chloroflexi)、浮霉菌门(Planctomycetes)和疣微菌门(Verrucomicrobia)为优势菌门,其相对丰度分别为 31.0%~33.7%、14.8%~17.7%、4.6%~8.7%、7.0%~8.3%、6.1%~7.0% (图 2)。随着淹水时长的增加,耐涝基因型大豆根际中的变形菌门(Proteobacteria)、酸杆菌门(Acidobacteria)的相对丰度增加,但是绿弯菌门(Chloroflexi)、浮霉菌门(Planctomycetes)、疣微菌门(Verrucomicrobia)的相对丰度随着淹水时间的增加而减少。随着淹水时长的增加,涝害敏感基因型大豆中的酸杆菌门(Acidobacteria)相对丰度随着淹水时长的增加而增加,浮霉菌门(Planctomycetes)的相对丰度随淹水时间增加而减少(图 2)。在属水平上,在无淹水处理、淹水 1 d 和淹水 5 d 处理中,耐涝和敏感基因型大豆根际分别有 9、13 和 12 个属显著不同。在无淹水对照处理中,有 5 个属的相对丰度在耐涝基因型大豆中更高(图 3-a, b)。然而,在淹水 1 d 和 5 d 处理下,各有 4 个属的相对丰度在耐涝基因型中更高,其中 *Yonghaparkia* 和 *Unclassified-WD2101* 在 2 个处理中的耐涝害基因型中共同增高(图 3-c)。

为评价不同涝害处理下耐涝和敏感基因型大豆 OTU 相对丰度的差异,建立了负二项分布的广义线性模型。结果表明,相对于耐涝不淹水处理,耐涝淹水处理 1 d 和 5 d 的根际土壤样本中显著富集的 OTU 分别有 150 个和 290 个(图 4-a, b); 相对于敏感不淹水处理,敏感淹水 1 d 和 5 d 处理的根际土壤样

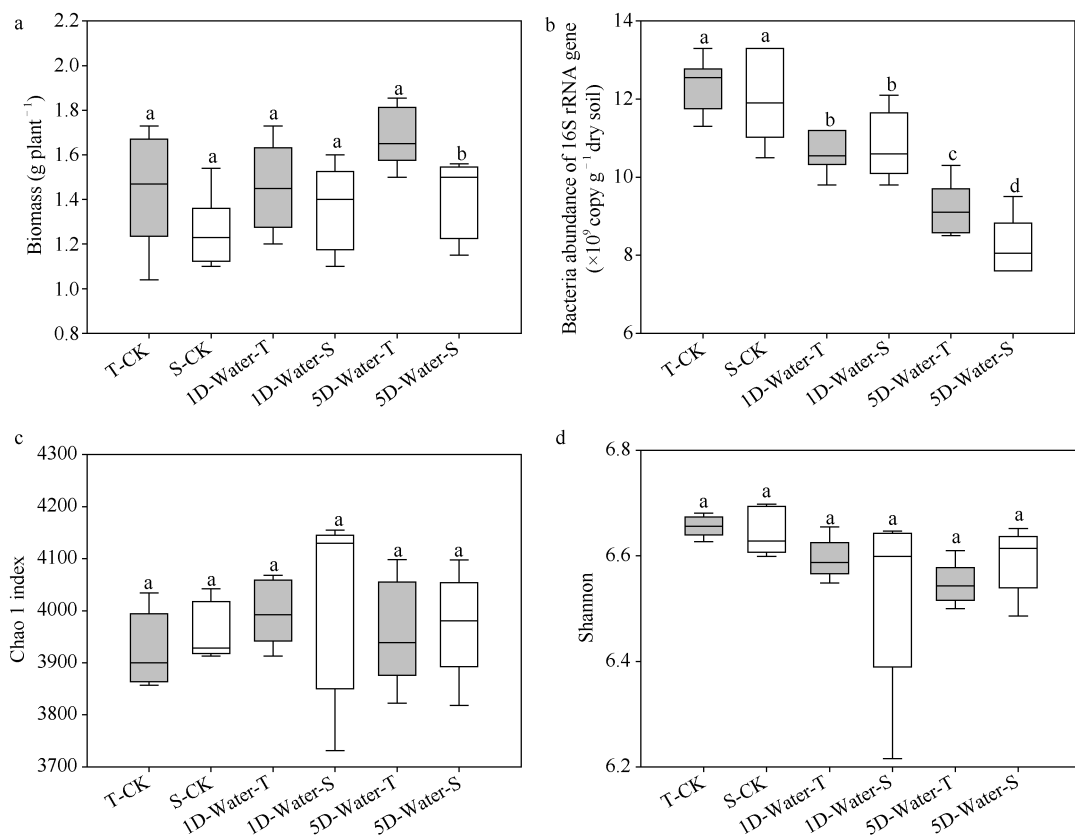


图 1 不同淹水时长对耐涝和涝害敏感基因型大豆 Chao 1 丰度(a)、Shannon 多样性(b)、生物量(c)和细菌丰度(d)的影响

Fig. 1 Effects of different waterlogging time on plant Chao 1 richness (a), Shannon diversity (b), biomass (c), and bacterial abundance (d) in W-T and W-S genotype soybeans

不同字母表示相同处理下 2 个品种间差异显著 ($P < 0.05$)。W-TCK: 耐涝品种淹水 0 d; W-SCK: 涝害敏感品种淹水 0 d; W-T1D: 耐涝品种淹水 1 d; W-S1D: 涝害敏感品种淹水 1 d; W-T5D: 耐涝品种淹水 5 d; W-S5D: 涝害敏感品种淹水 5 d。

Boxes superscripted by different letters indicate significant differences between two varieties under the same treatment ($P < 0.05$). W-TCK: waterlogging-tolerant variety without waterlogging; W-SCK: waterlogging-sensitive variety without waterlogging; W-T1D: waterlogging-tolerant variety under waterlogging for one day; W-S1D: waterlogging-sensitive variety under waterlogging for one day; W-T5D: waterlogging-tolerant variety under waterlogging for five days; W-S5D: waterlogging-sensitive variety under waterlogging for five days.

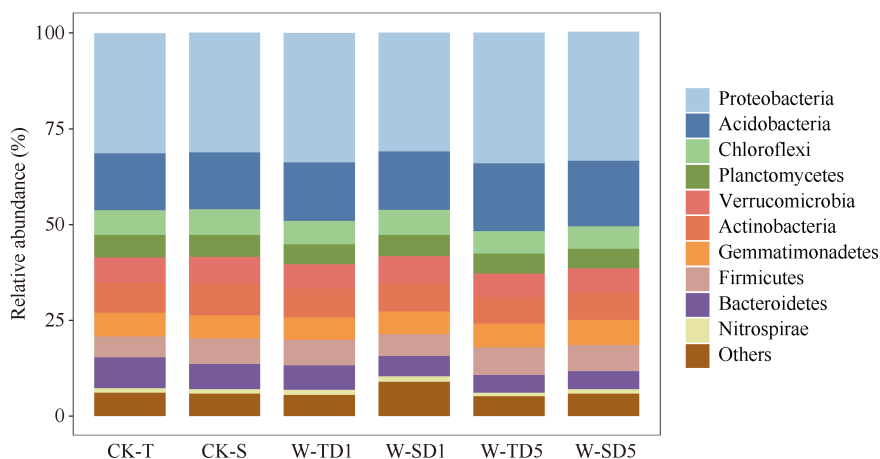


图 2 不同淹水时长处理下的门相对丰度

Fig. 2 Relative abundance of phylum under different waterlogging time

处理同图 1。Treatments are the same as those given in Fig. 1.

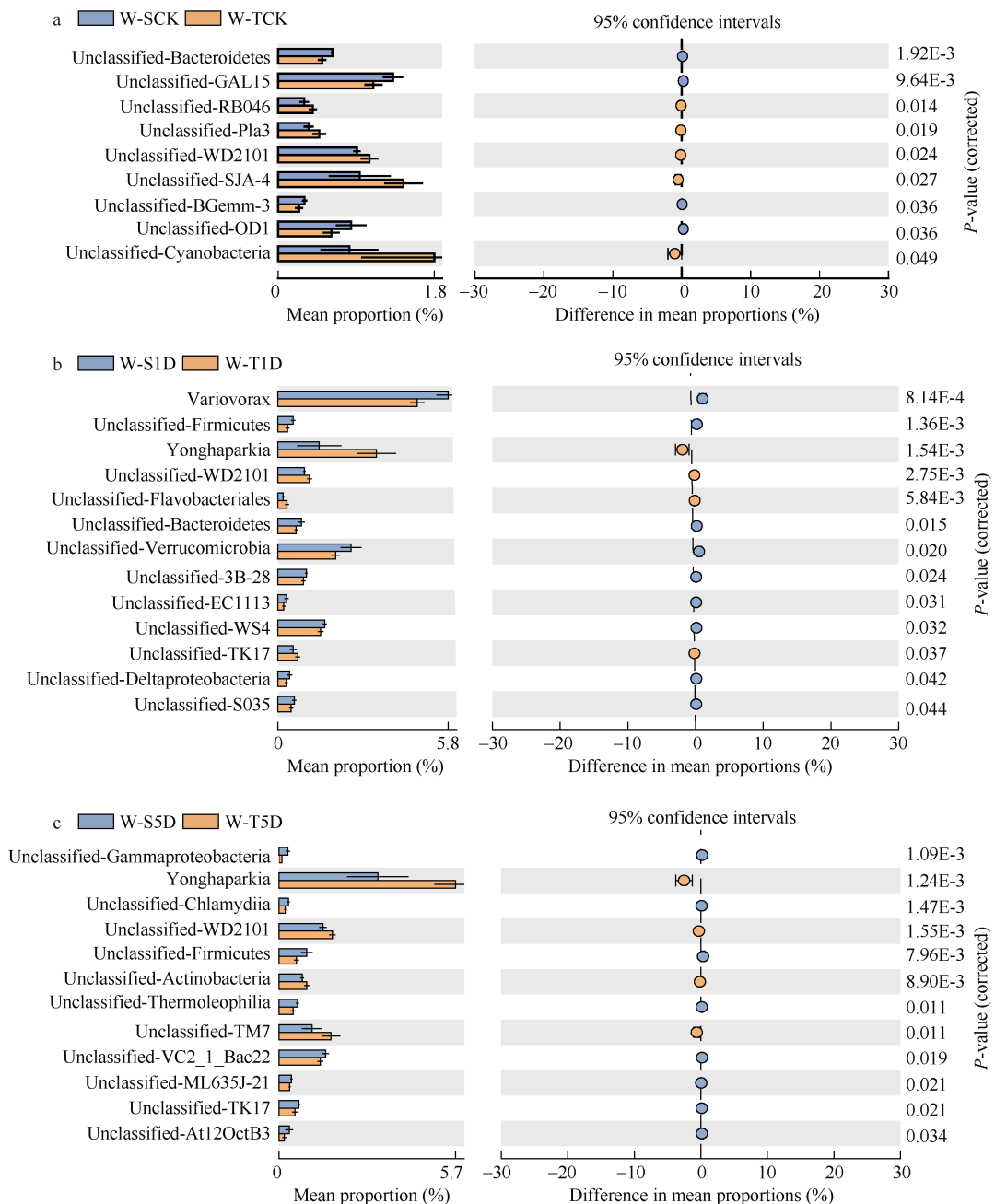


图 3 淹水时长 0 d (a)、1 d (b)、5 d (c) 下 W-T 和 W-S 基因型大豆根际细菌属的相对丰度

Fig. 3 Relative abundance of the genera of W-T and W-S genotype soybeans responding to 0 d (a), 1 d (b), and 5 d (c) waterlogging time

误差条表示 6 个重复样本的标准差。采用 Benjamini-Hochberg 法校正 P 值 ($P < 0.05$)。处理同图 1。

The error bars show the calculated standard variation of six replicates. Corrected P -values were calculated by the Benjamini-Hochberg false discovery rate approach at ($P < 0.05$). Treatments are the same as those given in Fig. 1.

本中显著富集的 OTU 分别有 100 个和 230 个(图 4-c, d)。通过 Venn 分析表明, 18 个 OTU 仅在淹水 1 d 和 5 d 处理中富集在耐涝基因型大豆根际土壤中(图 4-e)。其中 OTU218 (*Clostridium butyricum*)、OTU938 (0319-6A21)、OTU274 (*Clostridium*)、OTU2334

(*Desulfosporosinus*)、OTU1337 (*Geobacter*)分别在 2 个大豆基因型淹水处理下存在显著差异, 淹水 5 d 处理中, OTU274 (*Clostridium*)、OTU2334 (*Desulfosporosinus*)在耐涝基因型中的相对丰度较高(图 5)。

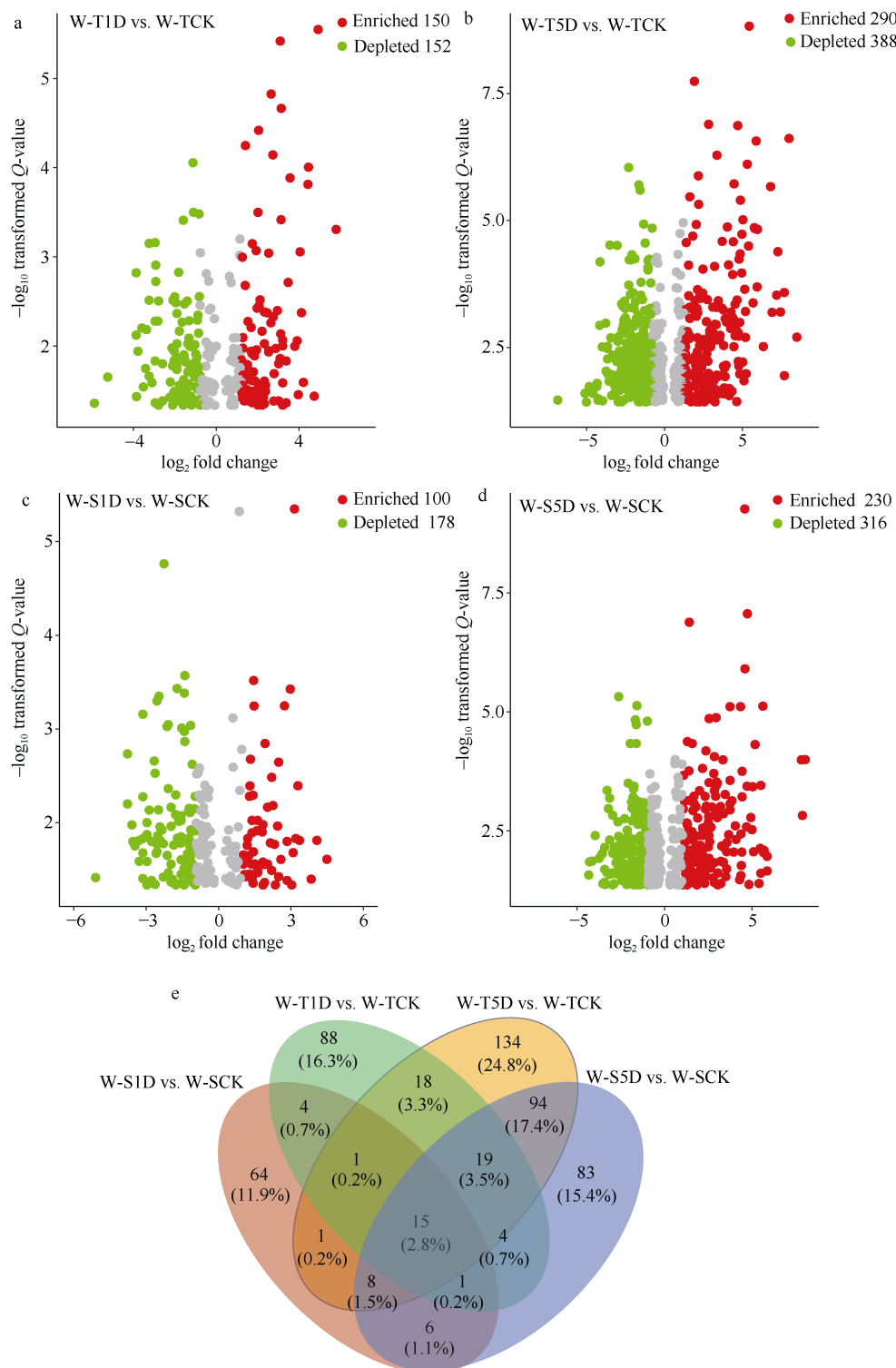


图 4 与无淹水对照相比, 不同淹水时长及大豆基因型富集和降低的 OTU

Fig. 4 Enrichment and depletion of OTUs included in the waterlogging one day and five days compared with the no-waterlogging soybean controls in soybean

a: 耐涝品种淹水 1 d 和不淹水的对比分析; b: 耐涝品种淹水 5 d 和不淹水的对比分析; c: 涝害敏感品种淹水 1 d 和不淹水的对比分析; d: 涝害敏感品种淹水 5 d 和不淹水的对比分析; e: 不同淹水处理下根际土壤细菌在 OTU 水平的 Venn 分析。处理同图 1。

a: comparison analysis of W-T variety under waterlogging for one day and no waterlogging; b: comparison analysis of W-T variety under waterlogging for five days and no waterlogging; c: comparison analysis of W-S variety under waterlogging for one day and no waterlogging; d: comparison analysis of W-S variety under waterlogging for five days and no waterlogging; e: Venn analysis of rhizosphere soil bacteria at genus level under different waterlogging time. Treatments are the same as those given in Fig. 1.

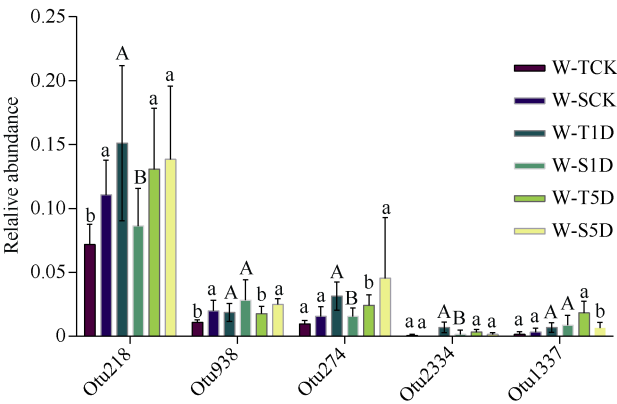


图 5 耐涝基因型大豆相关的 OTU 相对丰度
Fig. 5 Relative abundance of the OTU that associated to waterlogging tolerance soybean genotype
W-T: 耐涝基因型大豆; W-S: 涝害敏感基因型大豆。不同字母表示相同处理下 2 个品种间差异显著 ($P < 0.05$)。处理同图 1。
W-T: waterlog-tolerant soybean genotypes; W-S: waterlog-sensitive soybean genotypes. Bars superscripted with different letters indicate significant differences between the two varieties under the same treatment at $P < 0.05$. Treatments are the same as those given in Fig. 1.

2.3 根际土壤细菌群落的结构

PCoA 结果显示(图 6), X 和 Y 轴共解释了 65.2% 的群落变异, 并且 6 个处理分成 3 个大组, 其中不同淹水处理下的根际细菌群落聚集在一起, 说明淹水处理

理是改变根际微生物群落结构的主要因素。此外, 不同处理下 2 种基因型的根际细菌群落结构呈现显著差异, 而且这个差异随着淹水时长的增加也发生了变化(图 6 和表 1)。

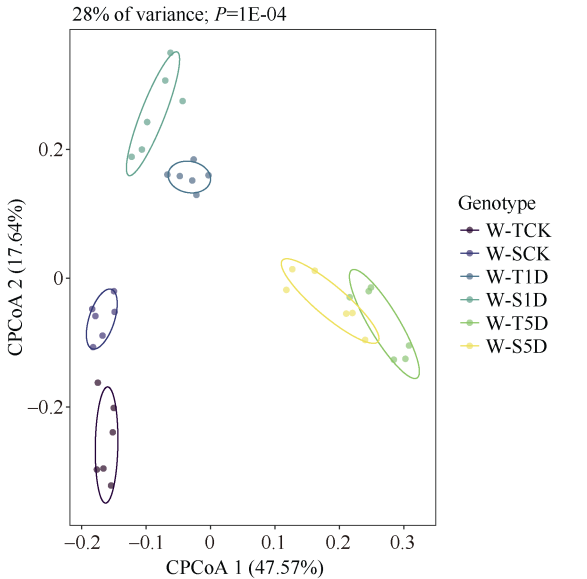


图 6 不同淹水处理下的根际土壤细菌群落主坐标分析
Fig. 6 Principal coordinate analysis of bacterial community in rhizosphere soil under different waterlogging time
处理同图 1。 Treatments are the same as those given in Fig. 1.

表 1 通过变异多变量方差分析(PERMANOVA)评估大豆基因型对根际细菌群落结构的影响
Table 1 Effects of soybean genotypes on rhizosphere bacterial community structure assessed by permutational multivariate analysis of variance (PERMANOVA)

配对比较 Pairwise comparison	统计值 F-value	决定系数 R^2	P 值 P-value
W-TCK vs. W-SCK	1.657	0.142	0.045*
W-T1D vs. W-S1D	1.970	0.165	0.003**
W-T5D vs. W-S5D	1.972	0.165	0.020*

处理同图 1。 **表示 1% 显著水平; *表示 5% 显著水平。
Treatments are the same as those given in Fig. 1. ** Significant at the 1% probability level; * Significant at the 5% probability level.

2.4 细菌群落的关联网络分析

网络关联分析表明, 在不同淹水处理下, 耐涝和敏感基因型大豆根际土壤之间的网络结构存在显著差异(图 7 和表 2)。随着涝害时间的增加, 耐涝基因型的正相关数、图密度和平均加权重度增加, 而在敏感基因型中网络的正相关数在淹水处理下更高。随着淹水时长的增加, 耐涝和敏感基因型的平均加权重度在淹水 1 d 和 5 d 处理下分别比不淹水有所增高。淹水 5 d 处理下, 耐涝基因型的正相关和负相关链接数都高于涝害敏感基因型。随着淹水时长的增加, 耐涝基因型网络变得更复杂, 值得注意的是敏感基因型中的网络也变得比不淹水时复杂。

3 讨论

3.1 不同淹水时长对根际土壤微生物多样性的影响

本研究旨在揭示涝害胁迫对耐涝基因型大豆和涝害敏感基因型大豆根际细菌的影响。当大豆遭受长时间淹水处理后, 细菌丰度都出现降低趋势, 且耐涝基因型高于涝害敏感型。该结果与 Azarbad 等^[47]的研究结果一致, 他们发现涝害急速降低了小麦根际土壤细菌的丰度。然而该结果与郭太忠等^[48]的研究结果相反, 他们发现涝害增加了玉米根际细菌的数量。造成这一不同的原因可能有 2 个: (1) 2 个研究

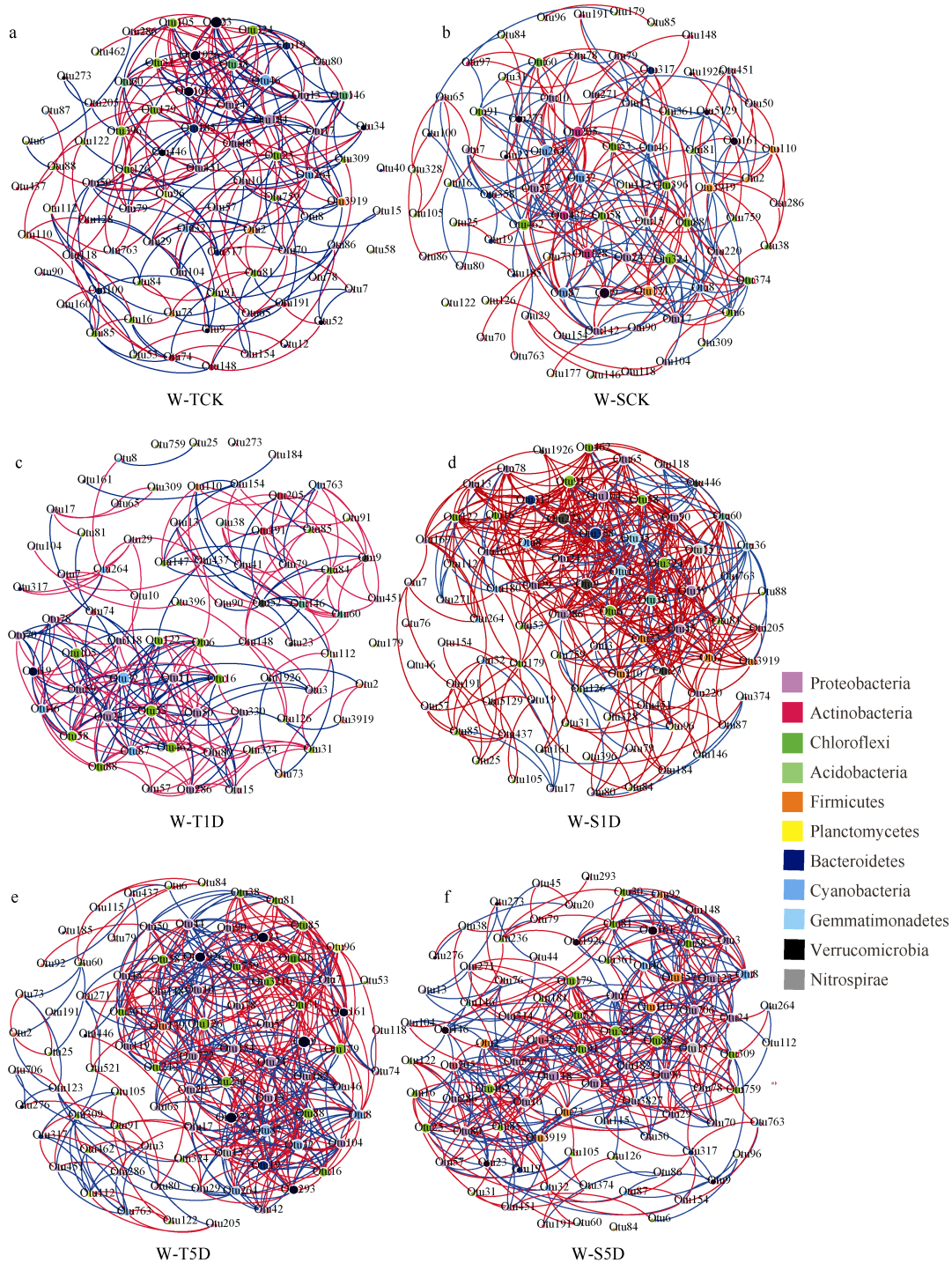


图 7 不同淹水时长和大豆基因型的根际细菌群落的共现网络结构

Fig. 7 Co-occurrence network of the rhizosphere bacterial community for different waterlogging time and soybean genotypes

a: 耐涝品种淹水 0 d 时根际细菌网络结构; b: 涝害敏感品种淹水 0 d 时根际细菌网络结构; c: 耐涝品种淹水 1 d 时根际细菌网络结构; d: 涝害敏感品种淹水 1 d 时根际细菌网络结构; e: 耐涝品种淹水 5 d 时根际细菌网络结构; f: 涝害敏感品种淹水 5 d 时根际细菌网络结构。图上不同的颜色节点表示不同的门。红色连接线表示 2 个节点正相关, 蓝色连接线表示 2 个节点负相关。处理同图 1。

a: co-occurrence network of the rhizosphere bacterial community of W-T variety without waterlogging; b: co-occurrence network of the rhizosphere bacterial community of W-S variety without waterlogging; c: co-occurrence network of the rhizosphere bacterial community of W-T variety under waterlogging for one day; d: co-occurrence network of the rhizosphere bacterial community of W-S variety under waterlogging for one day; e: co-occurrence network of the rhizosphere bacterial community of W-T variety under waterlogging for five days; f: co-occurrence network of the rhizosphere bacterial community of W-S variety under waterlogging for five days. Different color nodes represent different phyla. The red connection line indicates positive correlation between two nodes, and the blue connection line indicates negative correlation between two nodes. Treatments are the same as those given in Fig. 1.

表 2 根际细菌网络的拓扑结构

Table 2 Topological properties of rhizosphere bacterial networks

网络指标 Network metrics	W-SCK	W-TCK	W-S1D	W-T1D	W-S5D	W-T5D
节点数 Number of nodes	81	79	79	74	89	86
边数 Number of edges	338	346	536	317	521	579
正相关数 Number of positive correlation	218	216	433	224	321	353
负相关数 Number of negative correlations	120	130	103	93	200	226
平均路径长度 Average path length	3.816	3.058	2.626	3.688	3.192	3.195
图密度 Graph density	0.104	0.112	0.174	0.117	0.133	0.158
网络直径 Network diameter	10	7	7	9	9	9
平均聚类系数 Average clustering coefficient	0.641	0.594	0.72	0.688	0.638	0.649
平均加权度 Average degree	2.301	2.931	8.219	3.459	2.723	3
连接部件 Number of modules	4	4	5	5	3	3
模块化 Modularity	8.518	6.313	0.613	2.164	4.412	3.709

处理同图 1。Treatments are the same as those given in Fig. 1.

利用的方法不同,郭太忠等^[48]利用的是平板计数法,而该研究利用的是荧光定量 PCR 的方法。(2)作物种类的不同可能也会造成相反的结果。该研究中,耐涝品种的根际拥有更多的细菌数量,这也与 Azarbad 等^[47]的研究结果相似,涝害对不同作物基因型的根际细菌影响差异显著。这可能是因为土壤在淹水条件下,氧气大量减少,好氧细菌不易存活^[49-50],此外,淹水胁迫下耐涝基因型和敏感基因型根部不定根数量、通气组织强弱程度、根瘤数量、电导率和丙二醛含量等参数也可能造成耐涝品种拥有更多的细菌数量^[47,51-54]。最后,涝害胁迫强烈影响大豆植物的初级和次级代谢,且大多数改变的化合物都参与碳和氮的代谢以及苯丙烷途径,且这些改变在耐涝品种和涝害敏感品种中的差异是不一样的,其可能也是造成耐涝品种拥有更多的细菌数量的重要原因之一^[55]。

3.2 不同淹水时长对根际土壤微生物群落结构的影响

基于 PCoA 分析结果发现,涝害显著影响了大豆根际细菌群落结构(图 6)。这与前人研究的结果一致,涝害会对作物的根际土壤微生物群落结构产生影响^[56]。涝害可以对根际微生物造成直接的影响,当涝害导致厌氧时,对环境极为敏感的土壤微生物呼吸速率和活动减少,进而群落结构发生变化^[57-62]。此外,作物对涝害胁迫的响应也间接影响着根际微生物群落结构^[12]。已有研究表明,当作物受到涝害胁迫会影响地下碳输入的变化^[19-20],进而影响了根际微生物组^[63]。

本研究还发现,涝害显著改变了不同大豆基因型的根际微生物群落结构(表 1)。这是因为不同的植物基因型响应涝害胁迫的机制是不同的,比如,与涝害敏感大豆相比,耐涝大豆在淹水后,其根系生长、根系损伤以及气孔的速率表现出更高的适应性^[9,48]。此外,淹水对大豆植株根部的一级代谢和二级代谢均有较大影响。大多数改变的化合物涉及碳和氮代谢以及苯丙醇途径,而涝害敏感大豆和耐涝大豆之间的反应是不同的^[64]。以上的不同都会对根际微生物产生直接的影响,造成了涝害条件下 2 个品种根际微生物群落结构的显著差异。

基于属水平上的分析我们发现,在淹水时长为 1 d 和 5 d 时,耐涝基因型的细菌属 *Yonghaparkia* 和 *Unclassified-WD2101* 显著高于敏感基因型。其中,细菌属 *Yonghaparkia* 属于放线菌门,而前人研究表明,放线菌能够定殖在植物上促进根瘤细菌的分化,还能够促进土壤中的铁离子的吸收,增加植物抗性^[65-66]。*Unclassified-WD2101* 属于浮酶状菌纲,浮酶状菌纲的一些属可以在厌氧条件下处于厌氧氨氧化过程,而且还参与碳循环^[67-69]。因此,上述 *Yonghaparkia* 和 *Unclassified-WD2101* 在耐涝处理下相对丰度的增加,说明耐涝品种可能通过促进作物对碳氮元素及微量离子元素的吸收,进而增加大豆对涝害的抵抗力。然而,在 2 个基因型中差异表达 OTU 与耐涝性的相关是通过统计方式实现的,因此其在耐涝过程中具体的功能和作用还需要进一步进行验证。

基于 OTU 水平上的分析发现,淹水处理 5 d 时,耐涝基因型大豆富集了 OTU274 (*Clostridium*)和

OTU2334 (*Desulfosporosinus*) (图5)。*Clostridium* 是厌氧异养促生菌, 这些属的一些种具有可以定植在根系周围产生丙酸、分解纤维素的功能, 可能会帮助植物获取更多的营养物质适应胁迫^[70-71]。有研究报道 *Desulfosporosinus* 在土壤中的硫酸盐还原和碳循环中起着关键作用^[72], 然而该物种在耐涝害中的作用还没有报道。

3.3 不同淹水时长对不同大豆基因型细菌关联网络的影响

在农田环境中, 微生物物种是不可能单独生存的, 而是与其他自然界物种形成复杂的生态网络^[73]。网络分析的结构特性不仅可以揭示物种之间的复杂关系, 还可以表征生态网络结构的稳定性^[62,74]。本研究进行了关联网络分析, 以获得对细菌群落组成的更全面了解, 随着耐涝基因型的淹水时长的增加, 正相关数、图密度和平均加权重增加, 表明耐涝基因型的网络被复杂化, 而敏感基因型中观察到淹水处理也使得网络较为复杂。但是在水淹 5 d 处理下, 耐涝基因型的网络比敏感基因型更加复杂化, 耐涝基因型的正相关数、负相关数、平均度都高于涝害敏感基因型。这和我们的前期研究结果相似, 即非生物胁迫下, 抗性品种的网络结构更为复杂^[75]。前人研究表明, 高度连接的微生物群可以激发植物免疫系统, 加速激活对外界的防御^[76-78]。表明涝害使耐涝基因型的网络复杂化, 从而提高大豆抵御涝害胁迫的能力^[78-79]。

4 结论

不同淹水处理对不同基因型大豆的土壤根际细菌群落产生影响。随着淹水时长的增加, 2 个基因型大豆的细菌丰度逐渐降低, 且在淹水时长为 5 d 的时候也出现了显著差异, 耐涝基因型的细菌丰度高于涝害敏感型基因的细菌丰度。耐涝基因型大豆在淹水处理到达 5 d 后富集了 *Yonghaparkia* 属和 *Unclassified-WD2101* 属以及 OTU274 (*Clostridium*) 和 OTU2334 (*Desulfosporosinus*), 这些物种的富集可能与耐涝相关, 但其在耐涝过程中具体的功能和作用还需要进一步进行验证。此外, 涝害胁迫复杂化耐涝基因型大豆的网络结构, 这可能提高土壤细菌群落抵御其他生物和非生物因素胁迫的能力。

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