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·特邀综述·

水稻细菌性条斑病菌致病与水稻抗病机制研究进展

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摘要 水稻(*Oryza sativa*)细菌性条斑病(BLS)是由稻黄单胞菌稻生致病变种(*Xoc*)引起的一种重要检疫性病害。该病原菌兼具高度遗传多样性和强传播能力, 在种植集约化及气候变暖的双重驱动下, 在我国南方籼稻主产区持续扩散。该文从以下3个方面系统综述了*Xoc*-水稻互作机制研究进展。(1) 从病原层面解析了II型分泌系统(T2SS)、III型分泌系统(T3SS)及胞外多糖等关键毒性因子的致病机制, 揭示了致病小种的分化规律; (2) 从寄主层面阐明了PTI/ETI介导的抗病信号通路, 综述了抗病(*R*)基因克隆与感病(*S*)基因编辑研究进展; (3) 展望了未来的研究方向, 将致力于深度整合多组学技术系统解析*Xoc*致病信号网络, 依托泛基因组学规模化挖掘具持久广谱抗性的*R*基因, 创新构建*S*基因靶向编辑与植物免疫激活协同增效的绿色防控体系, 为BLS的可持续治理提供系统性解决方案。

关键词 细菌性条斑病, 稻黄单胞菌稻生致病变种, 致病机制, 先天免疫, 抗/感病基因

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水稻(*Oryza sativa*)作为全球约60%人口的主要能量来源, 年产量约7.8×10^8 t, 其中亚洲产区占比超过90%。我国作为全球最大的水稻生产与消费国, 种植面积稳定在3×10^7 hm^{2}以上, 产量占全球总量的28%, 连续30余年稳居世界首位。由稻黄单胞菌稻生致病变种(*Xanthomonas oryzae* pv. *oryzicola*, *Xoc*)引发的水稻细菌性条斑病(bacterial leaf streak, BLS)在江淮、长江流域及华南籼稻主产区呈区域性流行, 常年造成15%–25%的产量损失, 重发区域减产高达40%–60%, 已成为威胁我国水稻高产稳产的关键因素之一(方妍力等, 2024)。

1 我国水稻种植分布

我国水稻品种具有典型的广域生态适应性, 种植空间覆盖除青藏高原高寒区以外的全部农业生态区。据统计, 水稻栽培覆盖31个省级行政区, 地理跨度北起黑龙江漠河(53°33'N), 南至海南三亚(18°09'N), 垂直分布从海拔1.5 m (长三角滨海圩田)至2 000 m (云南红河梯田)。依据《中国水稻种植区划》, 综合自然生态因子(热量、水分、日照、海拔和土壤)、社会经济条件(行政区划、人口、土地资源和生产基础)及稻作特点(种植制度、品种类型、耕作方式和栽培技术), 全国划分为六大稻作区: 华南双季稻稻作区、华中双单季稻稻作区、华北单季稻稻作区、东北早熟单季稻稻作区、西南高原单双季稻稻作区和西北干燥区单季稻稻作区(表1), 上述产区贡献全国98.7%的水稻总产(梅方权等, 1988)。

2 水稻细菌性条斑病

2.1 BLS分布

BLS作为具有强传播性的细菌性病害, 其流行史可追溯至20世纪初。该病害于1918年首次在菲律宾被发现, 随后蔓延至亚洲热带及亚热带地区(刘维等, 2022)。珠江三角洲地区于1953年首次监测到BLS疫

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表1 中国水稻生态种植区与细菌性条斑病(BLS)流行区的空间耦合关系

Table 1 Spatial coupling relationship between rice planting ecoregions and bacterial leaf streak (BLS) epidemic areas in China

中国稻作区	BLS主要发病区	BLS严重发病区
华南双季稻稻作区	海南; 广东和广西北部; 云南和福建南部	广东和广西南部; 福建北部
华中双单季稻稻作区	四川东北部; 安徽和江苏北部; 湖南和江西南部	湖北; 浙江; 上海; 湖南东北部; 江西北部; 安徽和江苏南部
华北单季稻稻作区	几乎无	几乎无
东北早熟单季稻稻作区	几乎无	几乎无
西南高原单双季稻稻作区	贵州; 云南西部和南部	湖南西北部; 四川西南部
西北干燥区单季稻稻作区	几乎无	几乎无

情, 标志着该病害侵入我国稻作系统。截至2024年, BLS已扩散至全国14个省级行政区的411个县(市、区), 形成以华南、华中及西南稻作区为核心的重灾带(表1)。在长江流域杂交晚稻种植区, BLS呈区域性大流行态势, 其爆发频率持续升高且危害程度日益加剧, 造成的经济损失已超越水稻白叶枯病(bacterial blight, BB), 成为威胁国家粮食安全的重要病害。

2.2 BLS侵染循环

*Xoc*主要为害水稻叶片, 通过气孔或伤口侵入叶肉组织后, 优先定殖于薄壁细胞。侵染初期, 在叶片上形成水渍状透明斑点, 病斑沿叶脉纵向扩展成4–6 cm半透明条纹。发病后期, 病斑逐渐褐变, 湿润条件下渗出蜜黄色菌脓, 呈鱼籽状排列, 干燥后形成琥珀状黄色小珠, 不易脱落。病害严重时, 许多条斑交叉相连, 融合成不规则的黄褐色至枯黄色大斑, 远观呈火红色景观。*Xoc*可在种子、稻草和田边杂草中越冬, 成为次年主要初侵染源, 通过风雨媒介实现田间短距离扩散, 并借助带菌种子调运进行跨区域传播, 导致BLS扩展蔓延(图1)。

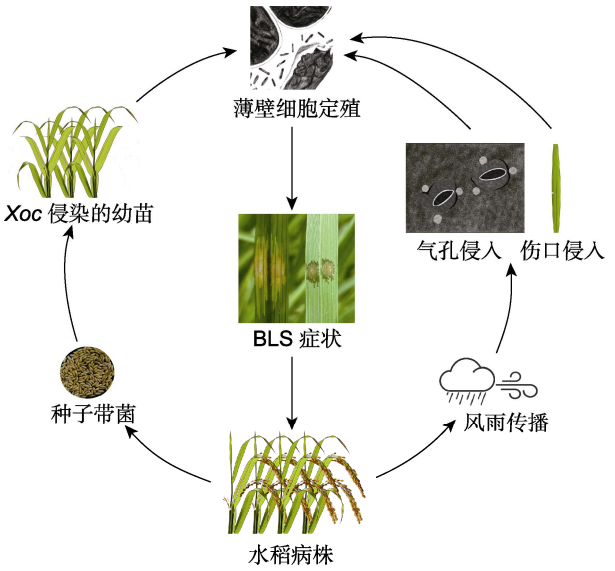

图1 稻黄单胞菌稻生致病变种(*Xoc*)侵染循环与水稻细菌性条斑病(BLS)传播途径示意图

Figure 1 Schematic diagram of *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*) infection cycle and rice bacterial leaf streak (BLS) transmission pathways

3 水稻细菌性条斑病菌

3.1 *Xoc*病原特征

*Xoc*隶属于黄单胞菌属(*Xanthomonas* spp.), 为革兰氏阴性短杆菌(0.7–2.0 μm × 0.4–0.7 μm), 具偏端单生鞭毛, 无芽孢及荚膜, 专性好氧代谢(Niño-Liu et al., 2006)。该菌分泌大量胞外多糖(extracellular polysaccharides, EPS), 在营养琼脂(nutrient agar, NA)培养基上形成亮黄色光滑菌落, 边缘整齐, 呈凸透镜状隆起(Niño-Liu et al., 2006)。其最适生长温度为25–30°C, 以蔗糖为最适碳源, 谷氨酸为最适氮源; 生理生化特性表现为过氧化氢酶阳性, 硝酸盐还原阴性, 淀粉水解阳性。

3.2 *Xoc*致病机理

3.2.1 II型分泌系统

II型分泌系统(type II secretion system, T2SS)是革兰氏阴性细菌中广泛存在的多蛋白复合物, 负责介导效应蛋白的跨膜转运。这些效应蛋白在病原菌营养获取、生物膜形成及致病过程中发挥关键作用(Naskar et al., 2021)。黄单胞菌属中T2SS结构具有显著异质性, 如柑橘溃疡病菌(*X. axonopodis* pv. *citri*, *Xac*)、

辣椒斑点病菌(*X. campestris* pv. *vesicatoria*, *Xcv*)和野油菜黄单胞菌(*X. campestris* pv. *campestris*, *Xcc*)中, T2SS同时存在Xps系统(11个*xps*基因编码)和Xcs系统(12个*xcs*基因编码), 而*Xoc*仅保留Xps系统(Lu et al., 2008)。其中*xpsE*作为Xps系统的核心基因, 其突变可显著削弱*Xoc*的毒力、游动性及胞外蛋白酶活性(Qian et al., 2013)。

T2SS分泌的细胞壁降解酶(cell wall-degrading enzymes, CWDEs)通过水解植物细胞壁组分, 促进病原菌侵入与定殖(Pfeilmeier et al., 2024) (图2)。在*Xoc*中, 胞外蛋白酶基因*ecpA*突变不仅导致胞外蛋白酶活性完全丧失, 而且显著降低其毒力与生长能力(Zou et al., 2012)。因此, 胞外蛋白酶表达水平已成为评价*Xoc*菌株毒力强弱的核心指标(Liang et al., 1994; Zou et al., 2012)。

3.2.2 III型分泌系统

由*hrp*基因簇编码的III型分泌系统(type III secretion system, T3SS)构成*Xoc*的核心毒力系统, 其决定着*Xoc*在感病水稻上的致病性以及在抗病水稻与非寄主上的过敏反应(hypersensitive response, HR) (Li et al., 2011; Xu et al., 2019, 2022) (图2)。通过其分泌的效应蛋白(type III secretion effectors, T3SEs)通常有2类: 一类为转录激活类效应子(transcription activator-like effectors, TALEs), 另一类为非转录激活类效应子(non-TALEs)。

TALEs通过核定位信号靶向寄主基因启动子区的效应蛋白结合元件(effector-binding element, EBE), 特异性激活抗病(resistance, *R*)/感病(susceptibility, *S*)基因表达, 以操控寄主的抗/感病性(Hummel et al., 2017)。TALE蛋白的功能差异取决于中心重复区单元数量及第12/13位氨基酸种类, 其中心区突变可使病原菌逃避寄主抗性识别(Ji et al., 2016; Read et al., 2016)。除典型的TALEs外, *Xoc*进化出干扰性TALEs (interfering TALEs, iTALEs) (如Tal3a和Tal3b), 通过拮抗植物免疫实现持久侵染(Ji et al., 2016; 徐夏萌等, 2023)。不同*Xoc*菌株携带的TALEs数量差异显著(7–33个), 如菲律宾BLS256 (28个)和中国RS105 (24个), 其组成多样性是致病力分型的核心指标(Scholze and Boch, 2011; Ji et al., 2014; Wilkins et al., 2015)。*Xoc*中已鉴定的关键TALEs成员包括Tal2g/Tal5d、Tal2h、Tal2a和Tal7等。Tal2g是首个明确功能的毒性效应子, 其缺失使BLS256菌株致病力显著降低(Cernadas et al., 2014; Tan et al., 2024)。Tal2a是首个明确功能的无毒效应子, 靶向水稻泛素羧基末端水解酶基因(*UCH*)并激活其表达, 其缺失对BLS256致病力无影响, 过表达则削弱致病力(Hummel et al., 2017; Tan et al., 2024)。Tal2b与Tal2c分别靶向黄烷酮3-羟化酶(flavanone 3-hydroxylase, F3H)基因*OsF3H03g*与*OsF3H04g* (二者与*OsS3H*均编码水杨酸羟化酶), 通过抑制水稻水杨酸(salicylic acid, SA)积累负调控广谱抗性(Tan et al., 2024)。

在*Xoc*中已鉴定出AvrRxo1、AvrBs2、XopN、XopC2、XopAP和XopAK等关键non-TALEs成员。其中, AvrRxo1通过干扰水稻维生素B6/ABA信号通路促进病原菌从气孔侵入, 并与XopC2和XopAP协同抑制丝裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)免疫通路(Liu et al., 2022a, 2022b; Tan et al., 2024)。在RS105菌株中, *avrBs2*基因缺失导致病原菌毒力显著降低; *xopAA*基因缺失在金刚30品种上毒力增强, 但是对日本晴和金禾2无显著影响; *xopN*基因缺失则未观察到毒力变化(Li et al., 2015)。在GX01菌株中, *avrBs2*与*xopN*基因存在累积效应, 二者共同维持菌株的全毒性(Liao et al., 2020)。这表明单个T3SEs的功能调控具有双重依赖性: 既受效应蛋白固有特性的影响, 又受水稻品种遗传背景的调控。

Xoc T3SEs的表达受寄主信号诱导, 并受HrpG-HrpX转录调控级联调节, 形成与侵染进程同步的时空表达模式(Teper et al., 2021)。该机制精准协调T3SEs的释放, 从而同步实现免疫抑制、资源劫掠及组织定殖等致病策略。

3.2.3 胞外多糖

EPS作为*Xoc*的核心毒性因子, 其生物合成受*gum*、*xan*和*wxoc*三大基因簇协同调控。该多糖通过包裹菌体形成黏质层, 协助病原菌逃避寄主免疫识别(如活性氧迸发和胼胝质沉积)并增强对环境胁迫的耐受性, 以诱导寄主易感性(Yun et al., 2006) (图2)。研究表明, *vemR*基因缺失导致*Xoc*致病性、游动性及EPS合成能力显著下降, 并且丧失在非寄主烟草(*Nicotiana*

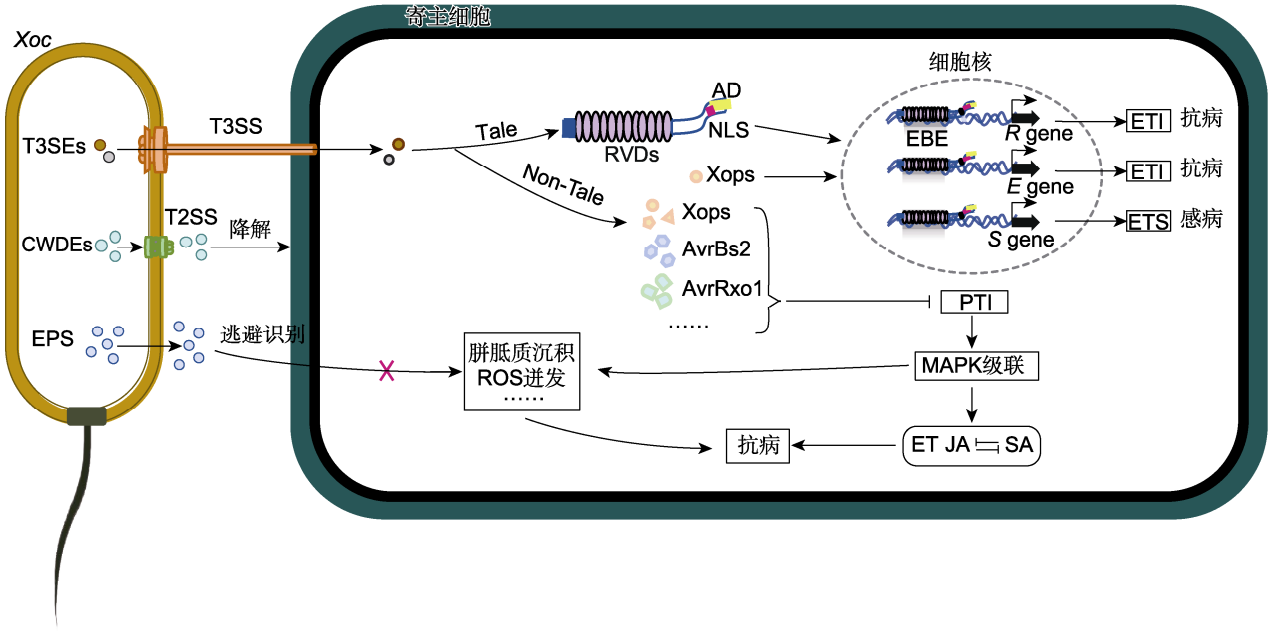

图2 *Xoc*与寄主水稻互作示意图

*Xoc*利用T2SS分泌CWDEs水解水稻细胞壁组分，促进病原侵染与定殖；利用T3SS向水稻细胞中注入T3SEs（TALEs和non-TALEs），TALEs通过核定位靶向寄主基因启动子EBE区，特异性激活*R*/*E*/*S*基因表达，触发ETI或ETS，non-TALEs协同抑制调控激素合成的PTI。*Xoc*分泌EPS包裹菌体形成黏质层，逃避ROS迸发、胼胝质沉积等寄主免疫识别。*Xoc*: 稻黄单胞菌稻生致病变种; T2SS: II型分泌系统; CWDEs: 细胞壁降解酶; T3SS: III型分泌系统; T3SEs: III型分泌效应蛋白; TALEs: 转录激活类效应子; non-TALEs: 非转录激活类效应子; EBE: 效应蛋白结合元件; *R* gene: 抗性基因; *E* gene: 执行者基因; *S* gene: 感性基因; ETI: 效应蛋白触发的免疫; ETS: 效应蛋白触发的感病; PTI: 病原体相关分子模式触发的免疫; EPS: 胞外多糖; ROS: 活性氧; Xops: 黄单胞菌外泌蛋白; MAPK: 丝裂原活化蛋白激酶; SA: 水杨酸; JA: 茉莉酸; ET: 乙烯; RVDs: 可变重复区; NLS: 核定位信号; AD: 酸性转录激活域。箭头表示激活作用，钝线表示抑制作用。

Figure 2 Schematic diagram of the interaction between *Xoc* and host rice

Xoc employs the T2SS to secrete CWDEs that hydrolyze rice cell wall components, facilitating its invasion and colonization; concurrently, it utilizes the T3SS to inject T3SEs (TALEs and non-TALEs) into rice cells. TALEs target the EBE region of host gene promoters through nuclear localization, specifically activating *R*/*E*/*S* gene expression to trigger ETI or ETS, while non-TALEs cooperatively suppress PTI that regulates hormone synthesis. *Xoc* secretes EPS to form a mucoid layer encapsulating bacterial cells, thereby evading host immune recognition including ROS burst and callose deposition. *Xoc*: *Xanthomonas oryzae* pv. *oryzicola*; T2SS: Type II secretion system; CWDEs: Cell wall-degrading enzymes; T3SS: Type III secretion system; T3SEs: Type III secretion effectors; TALEs: Transcription activator-like effectors; non-TALEs: Non transcription activator-like effectors; EBE: Effector-binding element; *R* gene: Resistance gene; *E* gene: Executor gene; *S* gene: Susceptibility gene; ETI: Effector-triggered immunity; ETS: Effector-triggered susceptibility; PTI: Pattern-triggered immunity; EPS: Extracellular polysaccharides; ROS: Reactive oxygen species; Xops: *Xanthomonas* outer proteins; MAPK: Mitogen-activated protein kinase; SA: Salicylic acid; JA: Jasmonic acid; ET: Ethylene; RVDs: Repeat-variable diresidues; NLS: Nuclear localization signal; AD: Acidic activation domain. Lines with arrows mean activation while blunt lines mean repression.

tabacum)上激发HR的能力(Cai et al., 2022); *fimO*、*pilY*和*xopQ*基因突变可诱导EPS合成量显著高于野生型菌株(周丹等，2011); RpfG则能调控EPS合成，促进菌株毒力和生物膜形成(Zhang et al., 2013)。有意思的是，EPS合成缺陷型突变体在寄主水稻上的毒力显著减弱，但其过量合成菌株并未表现出毒力增强(周丹等，2011)，表明EPS是*Xoc*致病必要但非充分因子。

3.3 *Xoc*致病小种致病型分化

在多种变异驱动因子的差异化作用下，*Xoc*菌株发生适应性演化，其致病型分化呈现显著的区域性特征，

导致抗BLS水稻品种的抗性具有区域特异性。

刘友勋等(2004)利用窄叶青等5个鉴别品种，将南方4省75个*Xoc*菌株划分为7个致病型(0–VI)。福建以III、IV型菌为主，江西以III、VI型菌为主，湖北以II、III型菌为主，湖南无显著优势菌群。郭亚辉等(2004)通过孕穗期剑叶针刺接种法，检测南方稻区62个菌株的致病力，并划分为6个致病型(C1–C6)。其中C1、C2致病力较弱但占比最高; C5、C6致病力最强; C3、C4因专化性互作明显，强弱难分。陈志谊等(2009)利用6个鉴别品种，将江苏徐淮地区82个菌株分为8个致病型，第1、2致病型为优势小种。王绍雪等(2010)基于西南地区75个菌株致病力反应，鉴定出13个致病型(C1–C13), C9为云贵川3省共同优势种。张荣胜等(2011)采用苗期注射与成株期针刺双接种法，将5省71株菌株划分为苗期18个致病型和成株期13个致病型，苗期优势小种为C1，成株期优势小种为C10。何涛等(2014)对安徽72株菌株监测后划分为6个致病型(I–VI)，其中强毒性的I型出现频率较高。周丽洪等(2014)基于212株菌株与6个抗性基因品种互作，鉴定出35个致病型，其中1、2号为优势种。李信申等(2017)将江西129株菌株划分为9个致病型(C1–C9)，各稻区优势种群多为强致病力的C3型或C3+C2型组合。杨俊等(2020)对云南86株菌株进行分析后鉴定出9个致病型(I–IX)，其中I型为优势菌群。

上述结果表明，不同地理来源的*Xoc*菌株致病型存在显著分化，且其致病力差异与地域特征密切相关。推测其潜在机制可能涉及各水稻主产区地理气候条件异质性、栽培品种持续更新与遗传背景演变，以及耕作制度的区域特异性差异等多种因素的综合作用。

4 水稻抗性机制

4.1 水稻免疫应答

水稻通过由病原体相关分子模式(pathogen-associated molecular patterns, PAMPs)触发的免疫(pattern-triggered immunity, PTI)和效应蛋白触发的免疫(effector-triggered immunity, ETI)构成双层防御系统以抵抗病原菌入侵(Jones and Dangl, 2006; Xu et al., 2022; Jin et al., 2023) (图3)。PTI作为基础防御，通过模式识别受体(pattern recognition receptors, PRRs)感知几丁质和鞭毛蛋白等PAMPs，激活MAPK信号通路，诱导活性氧迸发、胼胝质沉积及防御相关基因的表达(Yamada et al., 2017; Deb et al., 2020; Wang et al., 2020b)。ETI则通过核苷酸结合域-富含亮氨酸重复序列(nucleotide-binding domain leucine-rich repeat containing, NLR)蛋白特异性识别病原菌T3SEs (如TALEs)，触发HR和系统性抗性，其防御强度显著高于PTI (Jones et al., 2024; Yu et al., 2024)。Liang等(2025)揭示了一种水稻中先前未知的PRA-Rab转运机制：激活的NLRs可协同增强PTI，而PTI又反馈强化ETI，表明PRRs和NLRs在植物免疫系统中存在显著的协同互作关系。具体而言，水稻广谱抗病NLR免疫受体蛋白通过保护初级防御代谢通路免受病原菌攻击，协同整合PTI和ETI两层免疫系统，这揭示了赋予水稻广谱抗病性的一种新机制。

PTI激活的MAPK级联信号通过调控SA、茉莉酸(jasmonic acid, JA)和乙烯(ethylene, ET)等激素的合成，形成复杂的交叉调控网络(刘艳艳等, 2023)。其中，SA与JA信号通路存在显著拮抗：SA通过降解JA通路关键转录因子(如MYC2)抑制其活性，而JA则通过拮抗SA信号通路的关键组分削弱寄主对细菌性病害的抗性(Caarls et al., 2015)。研究发现，过表达SA信号基因*MPKK10.2*或*GH3-2*可显著增强水稻对*Xoc*的抗性(Fu et al., 2011; Ma et al., 2017)。外源喷施茉莉酸甲酯(MeJA)后接种*Xoc*，发现水稻JA途径相关基因*AOS2*、*LOX2*和病程相关基因*PR10*的表达上调，同时ET途径相关基因*EIN2*的表达下调(丁法等, 2023)。抗性品种与感性品种的差异响应源于SA途径相关基因、ET途径相关基因*ERF70*和病程相关基因*PR1a*的表达调控特性以及信号通路敏感性的不同，这凸显了激素平衡时序性调控的关键作用。

为应对植物PTI反应，病原菌进化出能抑制PTI的T3SEs (如TALEs)，这些T3SEs触发感病性(effector-triggered susceptibility, ETS)。而水稻*R*基因编码的NLR蛋白通过特异性识别T3SEs，向下游免疫系统传递信号，从而激活植物的抗病反应(Chen et al., 2022a; Xu et al., 2022)。这种病原菌T3SEs与寄主NLR蛋白之间的动态博弈驱动了水稻与*Xoc*的协同进化，促成抗性基因的多样性，为培育持久抗病水稻品种奠定了遗传基础。

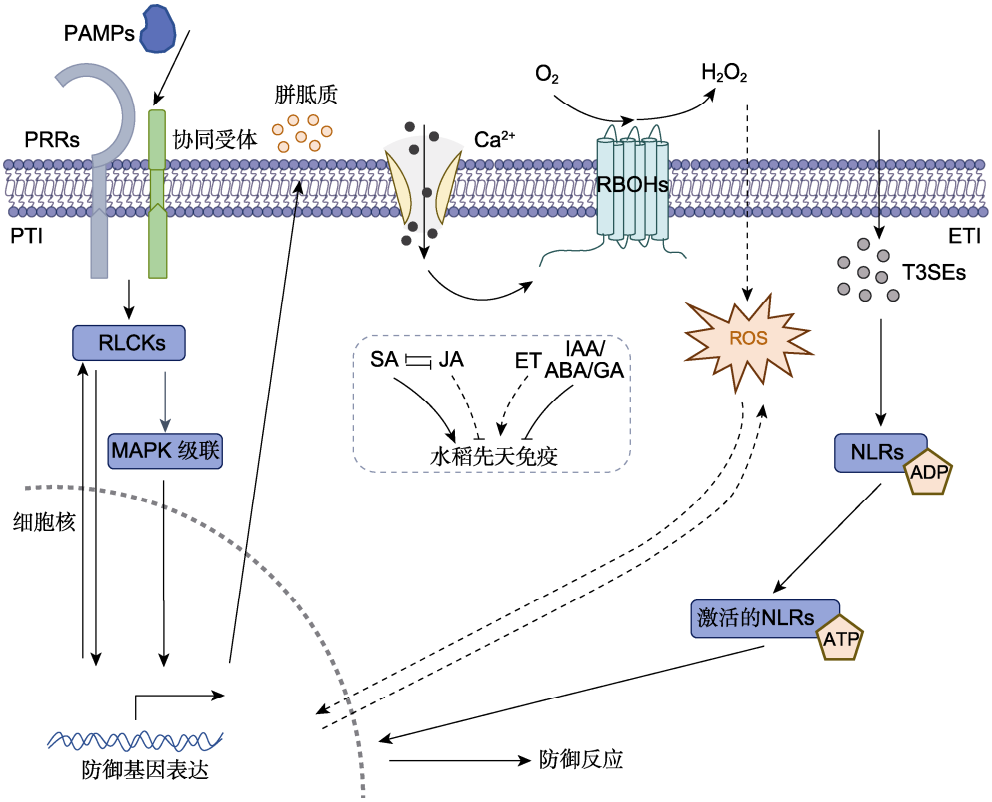

图3 水稻免疫应答网络示意图

*Xoc*与水稻互作中，PRRs识别PAMPs激活RLCKs，诱导Ca^{2+}内流、MAPK激活及转录重编程等防御信号。RLCKs磷酸化RBOHs的N端，被激活的RBOHs将O_2转化为H_2O_2，引起ROS迸发，促进防御基因表达。MAPK级联信号调控SA、JA和ET等激素合成，形成交叉调控网络以调节水稻抗性。NLRs识别T3SEs，整合细胞内信号事件触发HR等防御反应。PTI与ETI协同互作，共同增强免疫反应。*Xoc*: 稻黄单胞菌稻生致病变种; PRRs: 模式识别受体; PAMPs: 病原体相关分子模式; RLCKs: 受体样细胞质激酶; MAPK: 丝裂原活化蛋白激酶; RBOHs: 呼吸爆发氧化酶同源蛋白; ROS: 活性氧; SA: 水杨酸; JA: 茉莉酸; ET: 乙烯; NLRs: 核苷酸结合域-富含亮氨酸重复序列; T3SEs: III型分泌效应蛋白; HR: 过敏反应; PTI: 病原相关分子模式触发的免疫; ETI: 效应子触发的免疫; IAA: 生长素; GA: 赤霉素; ABA: 脱落酸。箭头表示直接(实线)或间接(虚线)激活作用，钝线表示抑制作用。

Figure 3 Schematic diagram of rice innate immune system

During *Xoc*-rice interactions, PRRs recognize PAMPs to activate RLCKs, inducing defense signals including Ca^{2+} influx, MAPK activation, and transcriptional reprogramming. RLCKs phosphorylate the N-terminus of RBOHs. The activated RBOHs convert O_2 to H_2O_2, causing ROS burst and promoting defense gene expression. The MAPK cascade regulates the synthesis of plant hormones SA, JA, and ET, forming a hormone cross-regulatory network that modulates rice resistance. NLRs recognize T3SEs and integrate intracellular signaling events to trigger defense responses such as HR. PTI and ETI act synergistically to collectively enhance immune responses. *Xoc*: *Xanthomonas oryzae* pv. *oryzicola*; PRRs: Pattern recognition receptors; PAMPs: Pathogen-associated molecular patterns; RLCKs: Receptor-like cytoplasmic kinases; MAPK: Mitogen-activated protein kinase; RBOHs: Respiratory burst oxidase homologs; ROS: Reactive oxygen species; SA: Salicylic acid; JA: Jasmonic acid; ET: Ethylene; NLRs: Nucleotide-binding domain leucine-rich repeat containing receptors; T3SEs: Type III secretion effectors; HR: Hypersensitive response; PTI: Pattern-triggered immunity; ETI: Effector-triggered immunity; IAA: Auxin; GA: Gibberellin; ABA: Abscisic acid. Arrows indicate direct (solid) or indirect (dashed) activation, flathead arrows indicate inhibition.

4.2 水稻BLS抗病/感病基因

水稻对BLS的抗性由主效基因介导的质量抗性与微效QTL (quantitative trait locus)调控的数量抗性共同决定(Wu et al., 2022)。主效基因凭借其广谱抗性及显著表型效应，在基因克隆与分子机制解析中具有明显的优势，但也存在已克隆基因数量有限、隐性遗传限制、持久性不足以及受我国相关生物安全法规限制应用等因素制约。微效QTL单个位点抗性效应较低且

克隆难度较大, 但其抗性不易因病原菌变异而丧失或不稳定(陈贤等, 2025)。

截至目前, 已克隆的BLS主效抗病基因共6个, 包括3个显性基因(*Xo1*、*Xo2*和*qBlsr5a*)、2个隐性基因(*bls1*和*bls2*)及1个非寄主抗性基因(*Rxo1*) (表2)。*Xo1*是首个被克隆的、源自水稻品种Carolina Gold Select的抗性基因, 其编码的NLR蛋白通过识别TALE蛋白的重复序列, 特异性抵抗来源于非洲的*Xoc*菌株(Triplett et al., 2016; Read et al., 2020)。*Xo2*被精细定位在水稻第2号染色体标记RM12941–M6-1间约110 kb的区域内, 推测NLR编码基因*Osa002T0115800*可能是其功能基因, 但其编码蛋白的具体功能或类别尚不明确(Chen et al., 2022b)。Xie等(2014)将*qBlsr5a*精确定位到30 kb范围内, 该区间内的*LOC_Os05g01710*是其候选基因, 但其编码蛋白的具体功能同样尚不明确。*Rxo1*是首个被克隆的、源自玉米(*Zea mays*)的非寄主抗性基因, 编码NLR蛋白。Rxo1识别病原菌T3SEs中的AvrRxo1并与之互作, 触发水稻免疫反应, 赋予其抗性。当侵染病原菌缺失*avrRxo1*时, 转基因表达*Rxo1*的水稻表现为感病(Zhao et al., 2005)。*bls1*及其等位基因*BLS1*均编码丝裂原活化蛋白激酶(OsMAPK6), 二者均负调控水稻对*Xoc*菌株JZ-8的特异性抗性。其中, *bls1*负调控广谱抗性, 而*BLS1*正调控广谱抗性(Ma et al., 2021)。*bls2*是一个控制普通野生稻抗源'DY19'对BLS抗性的主效隐性基因。该基因被精细定位在水稻第2号染色体标记RM13592–RM13599间约240 kb区域内, 这为*bls2*基因的最终克隆与功能解析奠定了基础(施力军等, 2019; 罗登杰等, 2021)。

在数量抗性位点研究方面, 目前已定位超过62个与BLS抗性相关的QTLs, 其中大多数尚处于初定位阶段(陈贤等, 2025)。Tang等(2000)利用亲本Acc8558和H358, 通过复合区间作图在6条染色体上初步定位了11个QTLs。Sattayachiti等(2020)基于236份水稻材料的全基因组关联研究(genome-wide association study, GWAS), 在8条染色体上鉴定出12个BLS抗性QTLs, 其中5个位点对多个*Xoc*菌株具有抗性, *qBLS5.1*和*qBLS2.3*表现出广谱抗性。Zhu等(2023)从747份水稻种质中定位到20个QTLs, 并初步确定了5个QTLs (*OsRBLS1–OsRBLS5*)的候选基因。Fang等(2023)基于水稻品种HZ、Nekken及其衍生的120个重组自交系(recombinant inbred lines, RILs)群体构建了单核苷酸多态性(single nucleotide polymorphism, SNP)遗传图谱, 检测到13个QTLs。位于12号染色体上的2个抗性QTLs效应显著, 可能为新的BLS抗性位点。随着对BLS抗性QTL研究的深入, 整合主效基因的强抗性与QTL的广谱持久抗性, 将是水稻抗BLS育种的关键策略。

在*Xoc*与水稻互作研究中, 已鉴定出多个被TALE蛋白靶向的*S*基因(表3), 这为抗病育种开辟了新方向。Xu等(2021)利用CRISPR/Cas9技术靶向编辑硫酸盐转运蛋白编码基因*OsSULTR3;6*启动子的

表2 水稻细菌性条斑病(BLS)抗性(*R*)位点与基因

Table 2 Resistance (*R*) loci and genes for bacterial leaf streak (BLS) in rice

来源	位点与基因	参考文献
玉米	*Rxo1*	Zhao et al., 2005
Minghui 63	*OsWRKY45-2*	Tao et al., 2009
ZH11	*OsMPK6*	Shen et al., 2010
Acc8558	*qBlsr5a*: 5号染色体ID73–ID79 (30 kb)	Xie et al., 2014
Carolina Gold Select	*Xo1*: 1090 kb	Triplett et al., 2016
ZH11	*AtNPR1*	Xu et al., 2017
TP309	*XCRK*: 1号染色体上	张玉霞等, 2018
Acc8558	*qBlsr3d*: *LOC_Os3g03570* (81 kb)	Wang et al., 2020a
DP3	*bls1*: 6号染色体上(21 kb)	Ma et al., 2021
DY19	*bls2*: 2号染色体RM13592–RM13599 (240 kb)	罗登杰等, 2021
X455	*Xo2*: 2号染色体RM12941–M6-1 (110 kb)	Chen et al., 2022b
WP1, 9311	*qBLS4.1*: 4号染色体上(521 kb)	韦敏益等, 2023

表3 水稻细菌性条斑病(BLS)感病(*S*)基因

Table 3 Susceptibility (*S*) genes for bacterial leaf streak (BLS) in rice

来源	基因	参考文献
Mudanjiang 8, Dongjin	*OsWRKY45-1*	Tao et al., 2009
Nipponbare	*OsSULTR3;6*	Cernadas et al., 2014
Nipponbare	*Os09g29100*	Cai et al., 2017
ZH11	*OsTFIIAγ5*, *OsTFIIAγ5*^{V39E}	Hui et al., 2019
Guihong 1, ZH11	*OsSULTR3;6*	Ni et al., 2021
IRBB10	*OsSULRT3;6*	Xu et al., 2021
ZH11	*OsF3H*$_{03g}$	Wu et al., 2022
ZH11	*OsBLS6.2*	Xie et al., 2023
Nipponbare, ZH11	*OsHXK5*, *OsSULRT3;6*	Wang et al., 2024

EBE区，显著增强了水稻对*Xoc*的抗性。Ni等(2021)在Guihong 1和ZH11品系中，同步编辑*OsSWEET11*、*OsSWEET14*和*OsSULTR3;6*基因启动子的EBE区，成功实现对*Xoo*和*Xoc*的双重抗性。Wu等(2022)通过突变2-酮戊二酸依赖性双加氧酶编码基因*OsF3H*$_{03g}$启动子的EBE区，阻断了Tal2b的靶向作用，显著提高了水稻对*Xoc*的抗性。Wang等(2024)证实，靶向编辑水稻己糖激酶基因*OsHXK5*启动子的EBE区，可有效抑制Tal10a介导的感病通路。基于Li等(2025)开发的新型内源基因精准标签技术，定向破坏TALE蛋白靶向的*S*基因EBE区，有望成为培育广谱抗BLS水稻品种的有效策略。

5 展望

*Xoc*致病力持续分化导致强毒力致病小种不断涌现，叠加全球气候变暖等因素扩大了其适生区域，使BLS发展为全球水稻生产中最具破坏力的细菌性病害之一(Timilsina et al., 2020; Chaloner et al., 2021)。近年来，*Xoc*致病机制与水稻BLS抗性研究虽取得一定进展(如*R*/*S*基因鉴定和QTL定位)，但相较于稻瘟病和白叶枯病，*Xoc*-水稻互作机制与抗病育种研究仍存在显著差距，主要表现在监测预警体系薄弱、致病机制解析不系统、广谱抗性基因稀缺、育种基因利用率低以及环境适应性评估缺失。为此，亟需从以下重点方向实现突破，以全面解析*Xoc*-水稻互作机制并构建高效可持续的绿色防控体系。

5.1 发展智能化监测预警技术

早期监测与精准诊断是水稻BLS防控的关键。传统人工巡查模式覆盖范围有限、时效性差，难以应对*Xoc*的快速传播与变异，亟需融合人工智能(AI)病害识别技术与高分辨率遥感监测技术，实现大范围、全天候的智能预警(Wang et al., 2021; Zheng et al., 2023; Mukherjee et al., 2025; Sharada et al., 2025)。同时，应开发基于*Xoc*泛基因组数据的高灵敏分子分型工具，实现致病型的快速鉴定与流行风险准确评估。需要指出的是，当前致病型研究多集中于成株期，苗期致病力分化机制及其与成株期的关联机制尚不明确(张荣胜等, 2011)。因此，系统解析*Xoc*在水稻全生育期的致病型演变规律，将为品种区域布局与轮作策略的精准设计提供理论支撑。

5.2 深度解析*Xoc*-水稻互作机制

在分子水平上深入解析*Xoc*-水稻的互作机制，是发掘抗病关键靶标、开辟抗性育种新策略的重要基础。未来应重点开展以下研究：基于比较基因组学与致病突变体库筛选，系统鉴定*Xoc*的关键毒力因子(如T3SEs)；整合原位转录组与代谢组分析，解析T3SEs在侵染过程中的动态表达模式及其与水稻的互作机制；依托泛基因组学鉴定核心TALE蛋白，阐明其操控水稻*S*基因表达的分子机理；系统研究SA、JA和ET信号通路的交叉调控网络，结合代谢流分析实时监测病原侵染过程中的激素动态变化，构建毒力因子与激素互作模型；设计SA/JA双响应启动子驱动抗菌肽表达，创制广谱抗性种质(Li et al., 2023)。

5.3 发掘抗性基因资源与推动育种应用

抗性基因挖掘是抗病育种的根本前提。当前亟需构建“泛基因组挖掘、精准编辑与合成免疫”协同整合的技术链，为水稻抗性改良提供新策略。首先，建立标准化*Xoc*接种与抗性鉴定体系，实现水稻种质资源BLS抗性的高通量评价；整合基因组变异数据与BLS抗性表型的关联分析，鉴定新型抗病基因或QTL位点(刘园园等, 2025)；借鉴其它水稻病害成熟的抗性基因发掘策略，挖掘优异基因资源，并利用BSA-seq结合水稻SNP芯片技术加速基因克隆。

抗病育种是实现基因资源向生产力转化的关键

环节。重点推进分子标记辅助选择、多基因编辑及抗病基因工程改造等研究，包括利用CRISPR/Cas9技术靶向修饰水稻*S*基因或其启动子EBE区(Xu et al., 2021)；基于结构生物学设计人工NLR蛋白广谱抗性结构域(Zhu et al., 2025)。最终，需在多生态点系统评估抗性材料的田间表现、温度适应性及抗性持久性，为选育抗病、高产、稳产水稻新品种提供可靠依据。

总之，水稻BLS的绿色可持续防控是一项系统工程，其突破依赖于植物病理学、基因组学及智能科学等学科的深度交叉融合，通过协同创新构建理论扎实、技术先进、可推广性强的精准防控体系，为我国及全球水稻安全生产提供坚实保障。

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Research Progress on Pathogenesis of *Xanthomonas oryzae* pv. *oryzicola* and Rice Resistance Mechanisms

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Abstract Rice bacterial leaf streak (BLS), caused by *Xanthomonas oryzae* pv. *oryzicola* (*Xoc*), is a significant quarantine disease. The pathogen exhibits both high genetic diversity and strong transmission capabilities. Driven by agricultural intensification and global warming, BLS has been progressively expanding across major indica rice-producing regions in southern China. This review systematically summarizes recent advances in *Xoc*-rice interaction mechanisms: (1) Pathogen perspective: elucidating pathogenic mechanisms of virulence factors (including T2SS, T3SS, and extracellular polysaccharides (EPS)) and pathovar differentiation patterns; (2) Host perspective: clarifying advances in PTI/ETI-mediated immunity signaling pathways, resistance (*R*) gene cloning, and susceptibility (*S*) gene editing; and (3) Future directions: proposing multi-omics approaches to decode *Xoc* pathogenicity networks, leveraging pan-genomics for large-scale mining of durable and broad-spectrum *R* genes, and constructing synergistic systems integrating *S* gene editing with immune activation to establish systematic solutions for sustainable BLS management.

Key words bacterial leaf streak, *Xanthomonas oryzae* pv. *oryzicola*, pathogenic mechanism, innate immunity, resistance/susceptibility genes

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