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·特邀综述·

水稻抗病调控机制研究进展

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摘要 水稻(*Oryza sativa*)是世界上最重要的粮食作物之一, 其产量影响全球粮食安全。然而, 水稻的各种病害对粮食安全构成极大威胁。其中, 稻瘟病、白叶枯病和纹枯病是影响全球水稻生产的3种主要病害, 培育具有广谱抗病性的水稻品种迫在眉睫。近年来, 水稻抗病调控机制研究取得了突破性进展。该文从水稻自身免疫反应以及抗病相关基因功能等方面综述了水稻抗病调控机制, 提出今后需解决的问题, 以期为水稻广谱抗病育种提供参考。

关键词 水稻, 抗病调控机制, 植物免疫响应

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水稻*(Oryza sativa)*是全球三大主粮作物之一, 其产量对于保障粮食安全至关重要(Yu et al., 2020)。然而, 水稻的各种病害对粮食安全构成极大威胁, 其中稻瘟病、白叶枯病和纹枯病3种主要病害严重制约水稻生产, 各种病害造成水稻产量损失平均可达30% (Liu et al., 2021b)。水稻病害的传统防治方法主要为喷洒农药, 但防治效果差, 施用成本高, 还会使病原菌产生抗药性。这使得原有病害更难控制, 不利于农业的可持续发展。克隆抗病基因并进行机制解析, 进而培育出抗病水稻品种是防治水稻病害的必要措施。

目前, 由于研究方法的改进和新技术的应用, 水稻三大病害研究取得了重大进展, 超过60个抗性基因被定位与克隆(Yang et al., 2022; Younas et al., 2024)。然而, 水稻植株对外来病原菌的防御反应机制尚未得到充分阐明。研究表明, 水稻在面对外来病原体入侵时会触发2层免疫系统, 包括病原相关分子模式(pathogen-associated molecular patterns, PAMPs)诱导的免疫反应机制(PAMP-triggered immunity, PTI)和病原菌效应蛋白(effector)诱导的免疫反应机制(effector-triggered immunity, ETI) (Lu and Tsuda, 2021), 并通过RNA修饰、泛素化修饰以及植物激素等途径偶联调控植株对病原菌的响应。本文对3种水稻病害的致病机制、水稻部分抗病防御机制以及抗性相关基因最新研究进展进行总结, 并提出水稻抗病领域的研究方向, 以期为水稻广谱抗病育种提供借鉴参考。

1 水稻主要病害

水稻在生长发育期间不可避免地受到一系列病原菌的侵害。据统计, 水稻有近20种常见病害, 其中稻瘟病、纹枯病和白叶枯病是全球传播最广泛、危害最严重的3种病害, 严重威胁水稻产量与稻米品质(Liu et al., 2021b)。

1.1 稻瘟病

稻瘟病是由稻梨孢菌(*Magnaporthe oryzae*)侵染引起的一种真菌型水稻病害。其病原菌通过形成功能性附着胞侵染水稻组织, 然后分化为侵染型菌丝, 在水稻细胞内大量繁殖。研究表明, 稻瘟病菌在侵染过程中通过形成活体营养表面复合体(biotrophic interfacial complex)和外侵菌丝膜(extrainvasive hyphal

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membrane) 2种结构向水稻细胞内释放大量的效应蛋白, 改变水稻的代谢和生理状态, 抑制免疫反应(Liu and Zhang, 2022)。稻瘟病在水稻整个生长期都可发生, 以叶瘟和穗瘟为主。稻瘟病在全球水稻种植区均有分布, 其中以亚洲和非洲水稻种植区病害最为严重。

1.2 白叶枯病

白叶枯病是一种世界性细菌型病害, 由稻黄单胞杆菌白叶枯致病变种(*Xanthomonas oryzae* pv. *oryzae*, *Xoo*)侵染导致。病原菌通常从气孔或创伤处侵入水稻组织, 在维管束中大量繁殖并分泌黄原胶堵塞筛管, 导致水稻营养运输受阻, 叶片迅速枯萎。研究表明, *Xoo*的III型分泌系统(Type III secretion system, T3SS)连通致病菌与宿主细胞, 与致病性密切相关(Shao et al., 2024)。细菌的效应蛋白能够通过T3SS进入宿主细胞, 影响细胞活性, 扰乱防御反应。一般可造成水稻减产10%–20%, 严重时甚至颗粒无收。近年来, 随着气候的变化, 灾害天气增多, 该病害有流行的趋势。

1.3 纹枯病

水稻纹枯病是由立枯丝核菌(*Rhizoctonia solani*)引起的一种土传性真菌病害。其病原菌主要通过2种方式侵染水稻: 一种是以菌丝形式从水稻气孔和伤口处直接侵入; 另一种是通过附着胞附着水稻叶片, 之后形成侵入钉完成侵染。Vidhyasekaran等(1997)发现立枯丝核菌在侵染过程中产生毒素, 毒素的主要成分是葡萄糖和甘露糖等糖类物质, 对水稻组织造成严重损伤, 在致病机制中起重要作用。由于立枯丝核菌潜伏在土壤和茬口中越冬, 随着气候的变化以及高产、矮秆良种的推广与种植, 其危害日趋严重(贺闽等, 2020)。

2 水稻先天免疫系统

水稻在长期与病原菌的斗争中进化出一套复杂的防御机制, 包括一系列生理生化和基因表达水平的变化, 亦称先天免疫系统。水稻免疫系统在机制上主要分为2类: PTI是由细胞膜表面的模式识别受体(pattern-recognition receptors, PRRs)识别PAMPs所激发的基础性免疫反应(Ngou et al., 2022); ETI是依靠抗病基因(resistance gene, R gene)编码的识别效应蛋白(R蛋白)识别病原菌分泌的效应蛋白激发的免疫反应(Jones et al., 2024)。在植物体生长发育过程中, 二者相互影响, 相互制约, 共同抵抗病原菌入侵。

2.1 PTI

PTI是植物基础抗性的重要组成部分, 对病原菌的防御响应具有广谱、持久和稳定的特点。研究表明, 介导PTI发生的水稻细胞表面受体主要分为RLKs (receptor-like kinases)和RLPs (receptor-like proteins) 2种类型(Boutrot and Zipfel, 2017)。这两类蛋白激活的防御反应包括丝裂原激活蛋白激酶级联信号通路、钙依赖蛋白激酶通路、活性氧(ROS)爆发以及防御激素产生等。目前在水稻中已鉴定的PRRs蛋白包括介导对白叶枯病菌抗性的XA21和介导对稻瘟病菌抗性的CEBiP等(Yu et al., 2024)。

2.2 ETI

ETI产生的抗性水平较高, 具有病原致病小种特异性, 是形式上更进化、抵抗病原菌更有效的免疫反应。病原菌效应子与R蛋白的识别阶段大体符合2种模型: 一种是R蛋白直接与相应的效应子作用, 进而激活下游抗病反应; 另一种则是效应子通过与第三方互作因子结合并修饰, 进而诱发抗病反应。此过程中植物胞内免疫受体(NOD-like receptors, NLRs)发挥重要作用。NLRs根据其N端结构域可分为3类——TNL (TIR-NLR)、CNL (CC-NLR)和RNL (CCR-NLR), 在识别过程中发挥传感器或助手的作用(Nabi et al., 2024)。在NLRs直接或间接识别病原菌效应子后, 激活相应病程相关蛋白(pathogenesis-related protein, PR)基因的表达, 产生免疫应答所需的植物激素(如水杨酸、茉莉酸和乙烯), 进而导致ROS爆发和细胞自噬, 最终诱发超敏反应(hypersensitive response) (Peng et al., 2021)。

3 水稻抗病调控机制

植物抵御病原菌的能力主要由R蛋白介导的抗病性和植物防御反应决定。与R蛋白识别特定病原体效应子所介导的水稻抗病性不同, 防御调节机制通常赋予植物对多种病原菌的抗性(Liu et al., 2021b)。其中, RNA修饰与RNA干扰、泛素化修饰和植物激素等途径通过级联调控机制激发水稻整体的防御反应, 对于提高水稻的广谱抗病性具有重要意义(图1)。

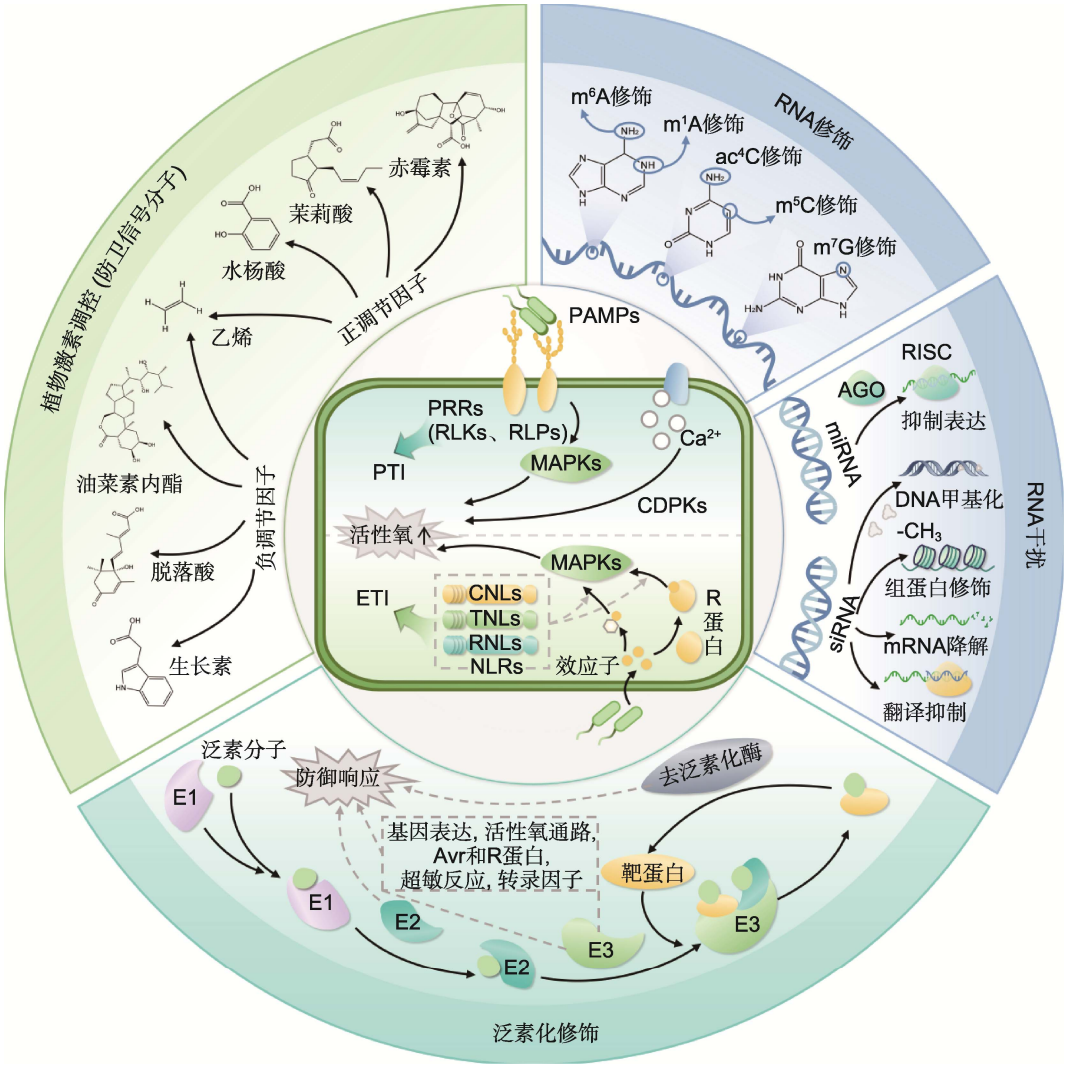


图1 部分水稻抗病调控机制

PAMPS: 病原相关分子模式; RLKs: 受体类激酶; RLPs: 受体类蛋白; PTI: 病原相关分子模式引发的免疫反应; ETI: 效应子激发的免疫反应; MAPKs: 丝裂原活化蛋白激酶; CDPKs: 钙依赖蛋白激酶; NLRs: 核苷酸结合位点和富含亮氨酸重复序列受体; CNLs: 具有N端卷曲螺旋结构域的NLRs; TNLs: 具有N端Toll/白细胞介素1受体结构域的NLRs; RNLs: 具有N端RPW8-CC结构域的NLRs; RISC: RNA诱导沉默复合体; AGO: 沉默机制蛋白

Figure 1 Part of the rice disease resistance regulatory mechanisms

PAMPS: Pathogen-associated molecular patterns; RLKs: Receptor-like kinases; RLPs: Receptor-like proteins; PTI: PAMP-triggered immunity; ETI: Effector-triggered immunity; MAPKs: Mitogen-activated protein kinases; CDPKs: Calcium-dependent protein kinases; NLRs: Nucleotide-binding site and leucine-rich repeat-containing receptors; CNLs: With N-terminal coiled-coil domains NLRs; TNLs: With N-terminal Toll/interleukin-1 receptor domains NLRs; RNLs: With N-terminal RPW8-like CC domains NLRs; RISC: RNA-induced silencing complex; AGO: Argonaute proteins

3.1 RNA修饰与RNA干扰

作为生物大分子，RNA不仅传递遗传信息，还作为基因表达调控的重要执行者，参与基因表达和生命活动。越来越多的研究表明，RNA及其化学修饰在调控水稻响应生物胁迫方面发挥重要作用。

RNA修饰是一类重要的表观遗传调控，通过在RNA分子的碱基或核糖上添加化学修饰基团调控基因表达，在植物防御反应过程中扮演重要角色。研究表明，N-甲基腺嘌呤RNA (m^6A)甲基化是真核生物中最常见的RNA修饰之一，其通过在腺苷酸的N6位上

添加甲基来改变mRNA结构, 影响mRNA的稳定性及翻译过程(Shinde et al., 2023)。Ren等(2022)发现在受稻瘟病侵染的水稻中, m^6A修饰在表达水平较低的基因上广泛出现, 通过改变靶RNA的二级结构, 介导水稻-病原菌相互作用中靶基因的空间和时间表达, 从而调控细胞内氨基酸代谢以及植物激素的合成与降解, 抑制水稻防御反应。此外, m^1A (N1-甲基腺苷)、m^5C (5-甲基胞嘧啶)和m^7G (7-甲基鸟苷)也是重要的RNA甲基化修饰类型。RNA乙酰化修饰已成为近年来RNA修饰研究新方向, 其中ac^4C被证实在水稻发育和抗逆反应中发挥重要作用。Lu等(2024)发现受稻瘟感染后水稻的ac^4C含量增加并富集于密码子第3位, 增强了与相应tRNA的相互作用, 提高了脂质代谢和茉莉酸合成相关mRNA的翻译效率, 增强水稻抗病性。

RNA干扰是由植物中一类具有特异性调控功能的小RNA (small RNA, sRNA)介导的基因沉默, 是植物抵抗病原菌的重要调节机制。根据生物合成途径植物内源sRNA可分为miRNA (micro RNA)和siRNA (short interfering RNA)两类(饶玉春等, 2024)。成熟的miRNA与其沉默机制蛋白AGO结合生成沉默复合体RISC, 与靶标mRNA高度互补, 进而抑制基因表达。siRNA则通过DNA甲基化、组蛋白修饰、mRNA降解和翻译来抑制基因表达沉默。Fan等(2020)发现在水稻抗病品种中, miR160和miR164受稻瘟病菌诱导表达量增高, 而miR398在稻瘟病菌侵染时表达水平降低, 在感病品种中其表达量不变, 表明不同的miRNA对ETI过程具有正调控或负调控作用。研究表明, miR444.2通过影响乙烯和生长素信号通路相关基因以及WRKYs和F-boxes等转录因子的表达来调控水稻纹枯病抗性(Feng et al., 2023)。*Pigm R*和*Pigm S*基因主效调控稻瘟病抗性与产量的平衡, 这2个位点产生的siRNA通过RNA依赖的DNA甲基化途径抑制*Pigm S*在花粉与稻穗以外的组织器官中表达, 从而提高其它器官的广谱抗病性(Deng et al., 2017)。

3.2 泛素化修饰

泛素化是指泛素在E1泛素激活酶、E2泛素结合酶和E3泛素连接酶3种酶介导的级联反应下特异结合到靶蛋白并修饰靶蛋白的过程。泛素化修饰不仅能调节细胞生长周期和激素信号转导等关键生理过程, 还在植物免疫应答和转录调控中发挥作用。目前, 水稻基因组中有6个E1泛素激活酶编码基因, 48个E2泛素结合酶编码基因, 1 500多个E3泛素连接酶编码基因, 以及95个去泛素化酶编码基因, 它们参与植物生长发育及非生物与生物胁迫响应等过程(Yan et al., 2024)。

E2泛素结合酶是泛素化修饰的重要组成部分, 在E3泛素连接酶与底物结合过程中起桥梁作用。研究表明, E2泛素结合酶可以通过改变靶蛋白的稳定性或酶活性参与水稻对病原体侵害的响应。例如, Liu等(2023)发现泛素结合酶OsUBC13通过促进水稻广谱抗病性正调节因子OsSnRK1a的泛素化修饰来减弱其活性, 从而负调节水稻免疫反应。泛素结合酶OsUBC26通过调节水稻免疫正调控因子OsWRKY45的表达, 并与E3泛素连接酶协同泛素化来自病原体的效应蛋白AvrPiz-t, 在水稻抗病反应中发挥重要作用(Liu et al., 2021a)。研究表明, 泛素结合酶OsUBC45正调控水稻PTI, 通过提高ROS的积累和抗性相关基因的表达水平增强水稻对稻瘟病和白叶枯病的广谱抗性。此外还发现, OsUBC45通过降解水稻水通道蛋白膜内在蛋白促进水稻的免疫反应(Wang et al., 2023)。

E3泛素连接酶是泛素化修饰过程中唯一具有特异性识别底物蛋白的酶, 且直接与靶蛋白互作。E3泛素连接酶广泛参与植物生长发育和胁迫应答过程, 种类丰富且具有庞大数量的E3决定了泛素化修饰对细胞活动的调控具有广泛性。E3泛素连接酶通过诱导PR编码基因的表达和影响ROS信号通路直接调控水稻PTI。例如, E3泛素连接酶相关基因*OsFBX156*过表达株系细胞内过氧化氢和酚类化合物积累增加, 进而使细胞壁增厚、防御能力增强, 表现出对多个稻瘟病菌小种具有广谱抗性(Zhao et al., 2024)。Wang等(2024)发现水稻E3泛素连接酶OsCIE1泛素化修饰OsCERK1受体蛋白, 使其活性被抑制, 从而防止免疫过度激活。当水稻受到真菌侵染时, 诱导OsCIE1磷酸化, 消除对OsCERK1受体蛋白的泛素化修饰, 进而启动免疫应答。部分E3泛素连接酶通过作用于Avr和R蛋白、超敏反应以及抗病相关基因的转录因子等参与水稻ETI (缴莉等, 2016)。例如, Shi等(2024)发现E3泛素连接酶IP17通过泛素化修饰特异性增强IPA1的转录激活活性, 促进稻瘟病抗病相关基因*WRKY45*的表达。Gao等(2020)研究发现, OsCUL3a蛋白负调控水稻细胞死亡和免疫功能, 水稻*OsCUL3a*基因敲除突变体细胞的ROS积累水平升

高, SA和JA信号通路被激活, 稻瘟病抗性增强。

泛素化过程是可逆的。回收靶蛋白上的泛素分子需要去泛素化酶参与。去泛素化酶在水稻防御响应中也发挥重要作用。Zou等(2023)发现去泛素化酶LMM22与斑点叶蛋白35 (SPL35)协作, 作为SPL35的关键调节因子, 使SPL35去泛素化, 抑制其降解, 从而在水稻抗病反应中发挥作用。Liu等(2023)发现, 去泛素化酶OsOTUB1.11可能通过激活水稻中SA与JA信号通路和增强水稻广谱抗病性正调节因子OsSnRK1a的活性来提高水稻抗病性。

3.3 植物激素调控

植物激素在生命活动中必不可少, 不仅是调控植物生长发育及衰老等生理过程的重要有机分子, 还在抗病和感病机制中扮演重要角色。乙烯(ET)、茉莉酸(JA)和水杨酸(SA)等植物激素广泛参与植物抗病过程。不同的植物激素信号通路在发挥自身功能的同时, 相互关联, 相互影响, 协同调控植物的生长发育及防御反应。

ET是一种常见的气态植物激素, 参与调节植物生长发育, 其介导的信号通路在水稻抗病反应中具有重要作用(Yang et al., 2015)。ET可作为正调节或负调节因子调控植物免疫反应。Moon等(2022)发现*Xoo*以免疫受体XA21依赖性方式诱导水稻特异性孤儿基因*Xio1*的表达, 而SA和ET诱导*Xio1*表达。Shen等(2011)研究表明, *OsEDR1*可诱导氨基环丙烷羧酸(ACC)的合成以及氨基环丙烷羧酸合成酶(ACS)家族基因的表达, 促进ET的积累, 进而抑制SA和JA相关基因的表达, 使水稻对*Xoo*的抗性降低。研究表明, 在稻瘟病病菌侵染水稻的过程中, 抗病材料的乙烯信号转导途径被激活, 乙烯积累量显著提高(Yang et al., 2017)。

SA在植物防御系统中发挥重要作用, 特别是使植物对病原体产生系统获得性抗性(饶玉春等, 2025)。在受到病原物侵染后, 植物体内SA大量积累, 导致PR蛋白表达, 增强了植物的抗病性。在水稻中, 内源SA水平增高和施用外源SA均可适度提高对病原体的抗性, 包括白叶枯病、稻瘟病等主要病害。Mohan Babu等(2003)用SA处理水稻, 发现其内源性SA水平增高3倍, 并检测到酚类物质和PR蛋白的水平升高。WRKY类转录因子OsWRKY45可被SA及其衍生物苯并噻二唑(benzothiadiazole)诱导。研究表明, 超表达*OsWRKY45*转基因水稻对稻瘟病抗性增强(Im et al., 2022)。Li等(2022)研究发现, *OsSGT1*编码SA葡萄糖基转移酶, 该酶催化SA转化为SAG, 可被*OsTGAL1*激活, 负调控白叶枯病抗性。

JA参与调节植物的生长发育和免疫反应。研究表明, JA信号通路与RNA沉默信号通路协同参与防御反应。病原菌侵染激活水稻JA信号, 导致其下游转录因子JAMYB的表达上调和转录激活活性释放。JAMYB结合并激活RNA沉默通路核心因子AGO18的启动子, 进而诱导AGO18表达, AGO18可以结合miR168以抑制其对AGO1的切割作用, 从而增强AGO1介导的水稻免疫反应(Wang et al., 2021b)。Ma等(2022)研究表明, 在水稻中超表达JA合成相关基因*OsAOS2*可上调*PR*基因的表达, 增强对稻瘟病菌的抗性。研究表明, OsLOX10和OsOPR10为JA合成途径的关键酶, 二者均正向调节水稻JA和SA信号通路, 促进水稻抗病(周永林等, 2022; 许丹洁等, 2024)。Gao等(2022)发现病变模拟基因*OsPHD1*的突变体对*Xoo*的抗性较野生型强, JA和MeJA在突变体中的积累增加。然而, 在突变体中JA信号通路基因表达下调, 这种调控机制可有效防止水稻过度防御。Suzuki等(2022)报道了MED25亚基, 其中功能缺失突变体*osmed25*对*Xoo*具有高抗性, *osmed25*负调控部分osmyc2非依赖性JA防御信号。

除以上3种激素外, 其它植物激素, 如赤霉素(GAs)、脱落酸(ABA)、油菜素内酯(BR)及生长素(IAA)在生物胁迫应答中也发挥重要作用。Nahar等(2013)在水稻抵抗禾生腐霉菌的药理实验中发现, 用GA和GA合成抑制剂处理可分别提高和降低水稻的抗病性。研究表明, 外源施加BR合成抑制剂, 以及BR缺陷型突变体均使植物对白叶枯病菌的抗性增强, 且BR介导的抗病过程通过SA与GA通路实现(De Vleesschauwer et al., 2012)。ABA作为重要的植物激素, 也参与植物的抗病反应。研究发现, ABA通过控制气孔开度来调节抗病性(Zhang et al., 2019)。IAA负调控水稻对病原菌的抗性。用IAA或2,4-D处理水稻, 会刺激*Xoo*增殖, 导致水稻感病(Figueroa-Macías et al., 2021)。

4 水稻抗病相关基因

4.1 稻瘟病

稻瘟病是影响全球水稻生产的重要病害, 以叶瘟和穗

颈瘟为主。研究表明, 调控水稻叶瘟和穗颈瘟的抗性基因分为3类。第1类为核苷酸结合位点-富含亮氨酸重复序列蛋白(NBS-LRR)类基因, *Pi5*、*Piz*、*Piz-t*、*Pi2*、*Pi9*、*Pi50*和*Pigm*均属于此类抗病基因。在识别到入侵的病原体后, 此类R蛋白检测分泌的病原体效应子, 产生ROS积累, 激活丝裂原活化蛋白激酶及防御激素信号等(Peng et al., 2021)。第2类是编码类受体蛋白激酶基因, *OsSERK1*、*OsCERK1*、*OsPRMT5*和*OsBIMK2*等为此类抗病基因。第3类抗病基因可编码富含脯氨酸结构域蛋白。例如, 隐性基因*pi21*的蛋白产物富含脯氨酸, 包含重金属结合结构域和蛋白互作结构域等功能域。与感病品种相比, 抗病品种Owarihatamochi的*pi21*基因中分别有21 bp和48 bp的缺失, 造成抗感差异(Fukuoka et al., 2009)。

在水稻基因组中, 除第3号染色体上尚未发现稻瘟病抗病基因外, 其余11条染色体上均定位到抗病基因, 其中第6、11和12号染色体上定位到的抗病基因最多。截至目前, 已鉴定到稻瘟病抗性基因140多个, 其中36个被克隆(Sahu et al., 2022), 大部分已克隆基因为NBS-LRR类基因(表1)。

表1 已克隆的水稻稻瘟病抗性基因

Table 1 Cloned resistance genes to blast in rice

基因名称	RAP号	编码蛋白类型	基因功能	参考文献
Pit	*Os01g0149500*	NBS-LRR	编码受体蛋白, 识别病原物	Hayashi et al., 2016
Pi64	*Os01g0781200*	NBS-LRR	编码受体蛋白, 识别病原物	Ma et al., 2015
Pish	*Os01g0782100*	NBS-LRR	编码受体蛋白, 识别病原物	Cheng et al., 2024
Pi35	*Os01g0782100*	NBS-LRR	*Pish*的等位基因	Fukuoka et al., 2014
Pi37	*Os01g0781700*	NBS-LRR	编码受体蛋白, 识别病原物	Lin et al., 2007
Pib	*Os02g0818500*	NBS-LRR	编码受体蛋白, 识别病原物	Xie et al., 2022
pi21	*Os04g0401000*	含脯氨酸蛋白	编码富含脯氨酸的蛋白, 加快免疫反应	Fukuoka et al., 2009
Pi63/*Pikahei-1*(*t*)	–	NBS-LRR	4号染色体抗病基因簇组成部分	Xu et al., 2014a
Pi50	*Os06g0286700*	NBS-LRR	6号染色体抗病基因簇组成部分	Su et al., 2015
Pi2	*Os06g0286700*	NBS-LRR	6号染色体抗病基因簇组成部分	Xie et al., 2019
Pi9	*Os06g0286700*	NBS-LRR	6号染色体抗病基因簇组成部分	Su et al., 2015
Piz-t	*Os06g0286700*	NBS-LRR	调控蛋白同源二聚化活性	Yu et al., 1991
Pigm	*Os06g0286700*	NBS-LRR	调控蛋白同源二聚化活性	Zhai et al., 2019
Pid3	*Os06g0330100*	NBS-LRR	调控防御反应调节相关的宿主因子活性	Zhou et al., 2019
Pi25	*Os06g0330100*	NBS-LRR	调控防御反应调节相关的宿主因子活性	Xu et al., 2014b
Pid3-I1	*Os06g0330100*	NBS-LRR	调控防御反应调节相关的宿主因子活性	Inukai et al., 2019
Pid2	*Os06g0494100*	受体蛋白激酶	编码植物凝集素类受体激酶	Wang et al., 2015b
Pi36	*Os08g0150150*	NBS-LRR	编码受体蛋白, 识别病原物	Liu et al., 2012
Pii	*Os09g0327600*	NBS-LRR	编码受体蛋白, 识别病原物	Takagi et al., 2013
Pi5	*Os09g0327600*	NBS-LRR	编码Pi5-1和Pi5-2蛋白, 蛋白互作调控免疫反应	Lee et al., 2009
Pi56	*Os09g0328951*	NBS-LRR	编码受体蛋白, 识别病原物	Liu et al., 2013
Pia	*Os11g0225100*	NBS-LRR	编码受体蛋白, 识别病原物	Okuyama et al., 2011
PiCO39	*Os11g0225300*	NBS-LRR	编码受体蛋白, 识别病原物	Césari et al., 2014
Pb1	*Os11g0598500*	NBS-LRR	编码受体蛋白, 识别病原物	Hayashi et al., 2010
Pik-h	*Os11g0639100*	NBS-LRR	编码Pikh-1和Pikh-2蛋白, 蛋白互作调控免疫反应	Zhai et al., 2014
Pi54rh	*Os11g0639100*	NBS-LRR	编码受体蛋白, 影响防御信号转导	Das et al., 2012
Pi54/*Pi-kh*	*Os11g0639100*	NBS-LRR	编码受体蛋白, 影响防御信号转导	Sharma et al., 2010
Pi54of	*Os11g0639100*	NBS-LRR	编码受体蛋白, 影响防御信号转导	Devanna et al., 2014
Pb2	*Os11g0682400*	NBS-LRR	编码受体蛋白, 识别病原物	Yu et al., 2022
Pi-k	*Os11g0689100*	NBS-LRR	11号染色体抗病基因簇组成部分	Zhai et al., 2011

表1 (续)

Table 1 (continued)

基因名称	RAP号	编码蛋白类型	基因功能	参考文献
Pik-m	*Os11g0689100*	NBS-LRR	11号染色体抗病基因簇组成部分	Ashikawa et al., 2008
Pik-p	*Os11g0689100*	NBS-LRR	11号染色体抗病基因簇组成部分	Wang et al., 2009
Pike	*Os11g0689100*	NBS-LRR	11号染色体抗病基因簇组成部分	Chen et al., 2015
Pi1	*Os11g0689100*	NBS-LRR	11号染色体抗病基因簇组成部分	Hua et al., 2012
Pita	*Os12g0281300*	NBS-LRR	编码受体蛋白，识别病原物	Bryan et al., 2000
Ptr	*Os12g0285100*	ARM重复序列的抗性蛋白	推测编码E3泛素连接酶	Zhao et al., 2018

RAP: 水稻基因组注释计划; NBS-LRR: 核苷酸结合位点-富含亮氨酸重复序列蛋白
RAP: Rice Annotation Project; NBS-LRR: Nucleotide-binding site-leucine-rich repeat protein

表2 已克隆的水稻白叶枯病抗性基因

Table 2 Cloned resistance genes to bacterial blight in rice

基因名称	RAP号	编码蛋白类型	基因功能	参考文献
Xa1	*Os04g0622600*	NLR类	NBS-LRR家族；诱导细胞凋亡	Yoshimura et al., 1998
Xa2	*Os04g0622600*	NLR类	*Xa2*、*Xa14*、*Xa31*(*t*)、*Xa45*(*t*)都是*Xa1*的等位基因，能被TALE激活抗性(效应子触发的抗性)并被TALE所抑制(效应子触发的感病性)	Ji et al., 2020
Xa14	*Os04g0622600*	NLR类		
Xa31(*t*)	*Os04g0622600*	NLR类		
Xa45(*t*)	*Os04g0622600*	NLR类		
xa5	*Os05g0107700*	其它	编码真核生物转录因子IIA伽马亚基	Iyer and McCouch, 2004
Xa7	*Os06g0280200*	Executor类	受AvrXa7诱导表达，激活超敏反应	Chen et al., 2021
Xa27	*Os06g0599600*	Executor类	受AvrXa27诱导表达，激活防御反应	Gu et al., 2005
xa13	*Os08g0535200*	SWEET类	调控铜离子在水稻体内的重新分布	Chu et al., 2006
Xa10	*Os11g0137600*	Executor类	受AvrXa10诱导表达，诱导细胞程序性死亡	Tian et al., 2014
xa41(*t*)	*Os11g0508600*	SWEET类	启动子与TALE蛋白的结合出现差错	Hutin et al., 2015
Xa21	*Os11g0569733*	激酶类	编码类受体蛋白激酶	Andaya and Ronald, 2003
Xa23	*Os11g0586701*	Executor类	受AvrXa23诱导表达，激活超敏反应	Wang et al., 2015a
Xa47(*t*)	*Os11g0688832*	NLR类	编码NLR类蛋白，受病原菌诱导表达	Xing et al., 2021
Xa3/*Xa26*	*Os11g0694850*	激酶类	编码LRR受体激酶，识别病原物	Cao et al., 2007
Xa4	–	激酶类	编码细胞壁相关激酶	Hu et al., 2017
xa25	*Os12g0476200*	SWEET类	编码MtN3/saliva家族成员	Liu et al., 2011

NLR: 核苷酸结合位点和富含亮氨酸重复序列受体; RAP和NBS-LRR同表1。

NLR: Nucleotide-binding site and leucine-rich repeat-containing receptors; RAP and NBS-LRR are the same as shown in Table 1.

4.2 白叶枯病

白叶枯病具小种特异性，相对于其它植物病害，白叶枯病抗性基因编码的蛋白类型丰富。根据抗病机理以及编码蛋白类型将白叶枯病抗性基因分为5类(彭小群和王梦龙，2022)。第1类基因编码NLR蛋白，其中*Xa1*基因编码NBS-LRR类蛋白，通过诱导细胞凋亡对白叶枯病产生抗性；第2类基因编码激酶蛋白，*Xa21*是编码LRR-RK类受体蛋白激酶的主效抗病基因，通过与*OsWARKY64*互作激活水稻防御基因的转录，增强水稻的抗病性；第3类基因编码SWEET蛋白，此类基因中*xa13*为隐形抗病基因，其编码的SWEET蛋白能够调控铜离子在水稻中的分布，而铜离子作为植物所需的微量元素能够有效抑制*Xoo*生长；第4类基因编码Executor蛋白，*Xa7*是最新克隆到的白叶枯病抗性基因，引发水稻超敏反应，阻止*Xoo*侵入；包含*xa5*在内的第5类基因通过编码其它蛋白增强水稻的抗病性。

目前，已报道和确认的水稻白叶枯病抗性基因至少有49个，包括32个显性基因和17个隐性基因，大部分白叶枯病抗性基因在第4和11号染色体上成簇分布，这些发现为后续白叶枯病抗性基因发掘明确了方向。而已克隆的白叶枯病抗性基因仅17个(表2)，仍有

大量抗病基因未被克隆。越来越多的证据表明，白叶枯病抗性属于多基因控制的数量性状(马路等, 2018)。深入挖掘水稻白叶枯病抗性基因将为理解白叶枯病抗性机制奠定坚实的基础，对水稻广谱抗性育种具有重要意义。

4.3 纹枯病

纹枯病抗性是由多基因控制的典型数量性状。目前已从水稻中分离和鉴定出多个纹枯病抗性基因。其中WRKY转录因子已被广泛研究。研究表明，*WRKY*基因通过与PAMPs效应蛋白直接或间接相互作用或通过MAPK调节来抑制或激活植物防御反应(Phukan et al., 2016)。多个WRKY转录因子形成一个顺次转录调控级联，进而调控水稻纹枯病抗性。此外，生理相关酶基因通过调节体内SA、JA和GA等植物激素的含量或调节ROS平衡来影响水稻纹枯病抗性。

截至目前，中国水稻数据库(https://www.rice-data.cn/)公布已鉴定和定位的纹枯病抗性基因58个。这些基因分布在12条染色体上，主要位于第3和11号染色体。近10年被发现和定位的纹枯病抗性基因大部分与植物激素调节、表观遗传调控和转录活性有关(表3)。对水稻纹枯病抗性基因进行挖掘与克隆，为解析纹枯病抗病机制奠定了坚实的基础，也为后续培育抗纹枯病水稻新品种提供理论依据。

5 问题与展望

水稻各类病害严重威胁粮食安全，在我国水稻生产中长期存在。自水稻全基因组测序完成以来，大批主效抗病基因被定位和克隆。而水稻基因组预测结果表明，这些基因多为小种专化性抗病基因，尤其缺乏真正经过长期田间试验鉴定的广谱抗病基因，如何在育种实践中进行广谱持久抗病育种存在不确定性。水稻抗病研究亟须开拓新思路。虽然在水稻分子育种中有效利用这些广谱抗病基因非常困难，但从具有优良农艺性状的水稻品种中鉴定这些基因的自然变异/等位基因、人工突变和基因组编辑技术将为广谱抗病基因挖掘提供重要方法。通过功能基因组学和测序技术不断挖掘与应用水稻抗病基因，进而完善水稻对病原菌的防御调控分子机制将是水稻病害防治的长期目标。

表3 部分水稻纹枯病抗性基因

Table 3 Partial resistance genes to sheath blight in rice

基因	RAP号	基因功能	参考文献
OsRLCK5	*Os01g0114100*	与丝氨酸羟甲基转移酶互作调控活性氧(ROS)水平	Wang et al., 2021a
OsPAL06	*Os02g0627100*	编码苯丙氨酸脱氨酶	Zhou et al., 2018
OsBON1	*Os02g0521300*	调控茉莉酸(JA)与水杨酸(SA)介导通路	Yin et al., 2018
OsPhyB	*Os03g0309200*	调控红光/远红光受体活性	Yuan et al., 2023
OsACBP5	*Os03g0243600*	调控JA与SA介导通路	Panthapulakkal Narayanan et al., 2020
OsUMP1	*Os03g0583700*	调控过氧化氢分解与蛋白分解代谢	Hu et al., 2023
Osoxo4	*Os03g0694000*	调控JA、脱落酸(ABA)与SA信号通路	Dong et al., 2021
OsGLP3-4	*Os03g0693800*	调控JA、ABA与SA信号通路	Li et al., 2015
RAVL1	*Os04g0581400*	参与油菜素内酯信号途径和合成途径基因表达	Yuan et al., 2018
OsWRKY45	*Os05g0322900*	SA信号通路介导的中心调节因子	Uji et al., 2019
OsWRKY53	*Os05g0343400*	正调控水稻油菜素内酯信号	Yang et al., 2023a
OsNYC3	*Os06g0354700*	α/β折叠水解酶家族蛋白，调控氧化还原酶活性	Cao et al., 2022
OsBZR1	*Os07g0580500*	调控DNA转录因子活性	Yuan et al., 2023
CYP716A16	*Os07g0518100*	调控JA与SA介导通路和ROS水平	Wang et al., 2022a
OsWRKY30	*Os08g0499300*	促进内源JA积累和病程相关蛋白(PR)基因表达	Wang et al., 2022b
OsGSTU5	*Os09g0367700*	增强抗氧化酶和谷胱甘肽还原酶活性	Yang et al., 2023b
KLP	*Os10g0512800*	调控转录辅助激活因子活性	Chu et al., 2021
OsSWEET14	*Os11g0508600*	调控对糖的非特异性运输	Kim et al., 2021
OsAFB3	*Os11g0515500*	调控生长素受体活性	Guo et al., 2021
OsASR2	*Os11g0167800*	靶向GT-1顺式作用元件，激活防御相关基因表达	Li et al., 2018
OsTrxm	*Os12g0188700*	硫氧还蛋白互作调控ROS清除	Park et al., 2019

RAP同表1。RAP is the same as shown in Table 1.

随着对水稻广谱抗病性的关注度越来越高，近年来，对RNA修饰与RNA干扰、泛素化修饰和植物激素调控等水稻抗病防御机制进行了大量研究。然而各种调控途径内部与不同调控途径之间仍存在大量空白，需进一步探明。此外，仅少数广谱抗性防御基因在介导水稻抗病的同时几乎或完全未造成产量损失，打破抗病基因与低产、劣质基因的连锁效应是抗病育种的当务之急(Li et al., 2019)。因此，深入揭示水稻抗病的分子调控网络，进一步加强对水稻先天免疫反应的解析，有助于推进水稻广谱抗病育种，打破抗病相关基因的应用壁垒。

作者贡献声明

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Research Progress on the Regulatory Mechanism of Rice Disease Resistance

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Abstract Rice (*Oryza sativa*) is one of the most vital food crops globally, and its yield plays a crucial role in ensuring food security. However, various diseases affecting rice pose significant threats to this security. Among these, rice blast, bacterial blight, and sheath blight are the three predominant diseases impacting global rice production. Consequently, there is an urgent need to breed and cultivate rice varieties with broad-spectrum disease resistance. In recent years, substantial advancements have been made in understanding the regulatory mechanisms underlying disease resistance in rice. This paper reviews these mechanisms from multiple perspectives, including the plant's intrinsic immune responses and the functional dynamics of resistance genes. Furthermore, it highlights pressing issues that require immediate attention to facilitate broad-spectrum disease-resistant breeding efforts for rice.

Key words rice, disease resistance regulation mechanism, plant immune response

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