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·热点评·

ZmFBL41$^{Chang7\text{-}2}$：玉米抗纹枯病的关键利器

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摘要 由真菌*Rhizoctonia solani*引起的纹枯病严重危害玉米(*Zea mays*)和水稻(*Oryza sativa*)等作物的安全生产。*R. solani*的宿主范围广且抗源少，加之相关的抗性机制研究有限，导致纹枯病的危害长期得不到有效控制。近期，中国科学家通过对318份玉米自交系进行全基因组关联分析，筛选到1个与纹枯病抗性相关的、编码F-box结构域蛋白的候选基因*ZmFBL41* (*GRMZM2G109140*)。ZmFBL41蛋白是SCF (SKP1-Cullin-F-box) E3泛素连接酶复合体的一员，能介导复合体对肉桂醇脱氢酶ZmCAD的降解，从而降低木质素的积累，使玉米易感纹枯病。玉米抗病自交系Chang7-2中，蛋白ZmFBL41$^{Chang7\text{-}2}$因2个关键氨基酸的变异，不能结合并降解底物ZmCAD，使木质素含量增加，从而提高玉米对纹枯病的抗性。该研究率先揭示了SCF复合体可通过降解肉桂醇脱氢酶来调控植物免疫反应的新型分子机制，为提高玉米及其它作物对纹枯病的抗性提供了重要理论依据和基因资源。

关键词 植物免疫, SKP1-Cullin-F-box，木质素，纹枯病，玉米，水稻

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由死体营养型真菌*Rhizoctonia solani*引起的玉米(*Zea mays*)、水稻(*Oryza sativa*)和大豆(*Glycine max*)纹枯病，以及马铃薯(*Solanum tuberosum*)黑痣病等是广泛流行的土壤传播疾病性作物病害。该病菌寄主范围广，包括禾本科、豆科和茄科植物等多达百种(Baruah and Lal, 1981)，常见致病优势菌群为AGs-1-IA (Ogoshi, 1987)。纹枯病在斯里兰卡被首次报道，之后传至全球，现已在许多国家爆发(Sharma et al., 2002)。该病害每年导致玉米和水稻产量损失达10%–40%，持续降雨条件下甚至达到100% (Singh and Sharma, 1976)。*R. solani*主要危害叶鞘，严重时危及穗子(Sharma et al., 2004)。纹枯病分布广、危害大且抗源少，因此，迫切需要挖掘作物的抗病基因，揭示其抗性机理并在生产中加以应用，对降低纹枯病的危害具有重要意义。

前人的研究表明，玉米对纹枯病的抗性属于多基因控制的数量性状(Li et al., 1995)。玉米的10对染色体上均有抗性相关的数量性状基因位点(quantitative trait locus, QTL)，并且在第6、7和10号染色体上的分布频率较高(Hooda et al., 2017)。然而，目前尚未克隆到控制玉米纹枯病抗性的主效基因。即使在模式作物水稻中，也仅发现转录因子基因*OsWRKY4* (Wang et al., 2015)和*OsWRKY80* (Peng et al., 2016)、几丁质酶基因*LOC_Os11g47510* (Richa et al., 2017)和CYP78A家族基因*OsBSR2* (Maeda et al., 2019)等少量基因调控纹枯病的抗性反应，这些基因介导的抗性机制也不清楚。

近期，山东农业大学储昭辉教授团队与其它单位的研究人员合作，通过全基因组关联分析(genome-wide association study, GWAS)，鉴定到28个与纹枯病抗性显著相关的SNP位点，这些位点分布于染色体1、4、7和8上的9个区段内。其中，位于第4号染色体的基因*ZmFBL41* (*GRMZM2G109140*)的第2个外显子内的SNP chr4.S_180199219与抗性的关联最为显著，因此推测该基因是调控纹枯病抗性的基因。

纹枯病抗性鉴定结果表明，转座子插入突变体*zmfbl41* (*mu1059763*)相比对照材料表现出较强的抗性。水稻中异源过表达*ZmFBL41*^{B73}后，纹枯病病症加重，表明*ZmFBL41*是纹枯病抗性反应的负调控因子。其编码蛋白含有F-box和LRR结构域，F-box结构

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域与ZmSKP1-1 (GRMZM2G417092)互作，形成一个E3泛素连接酶复合体SCF (SKP1-Cullin-F-box)，而LRR结构域与肉桂醇脱氢酶ZmCAD互作，介导SCF泛素连接酶复合体对底物ZmCAD的降解。转座子插入突变体*zmcad* (*mu1065184*)与对照相比更易感纹枯病；同样，水稻中敲除同源基因*OsCAD8B* (*LOC_Os09g23540*)后也更易感纹枯病，表明CAD蛋白是玉米和水稻纹枯病抗性反应的正调控因子。因此，玉米和水稻中存在相似的纹枯病抗性反应调控机制。

*ZmCAD*编码的肉桂醇脱氢酶催化木质素单体合成，是木质素合成途径的重要基因。ZmFBL41和ZmSKP1-1形成的SCF复合体通过降解ZmCAD降低木质素的积累。相应地，转座子插入突变体*zmcad*中的木质素含量降低，玉米更易感纹枯病；而转座子插入突变体*zmfbl41*中积累了较多的木质素，抗病性增强。此外，他们还进一步鉴定到ZmFBL41的1个自然等位变异ZmFBL41$^{Chang7\text{-}2}$ (ZmFBL41$_{E214G/S217R}$)，该变异能增强纹枯病的抗性。ZmFBL41$^{Chang7\text{-}2}$的214位(E→G)和217位(S→R)氨基酸发生错义突变，导致蛋白ZmFBL41$^{Chang7\text{-}2}$不能与ZmCAD互作，SCF复合体无法降解底物ZmCAD，使木质素含量增加，从而增强对纹枯病的抗性(Li et al., 2019)。

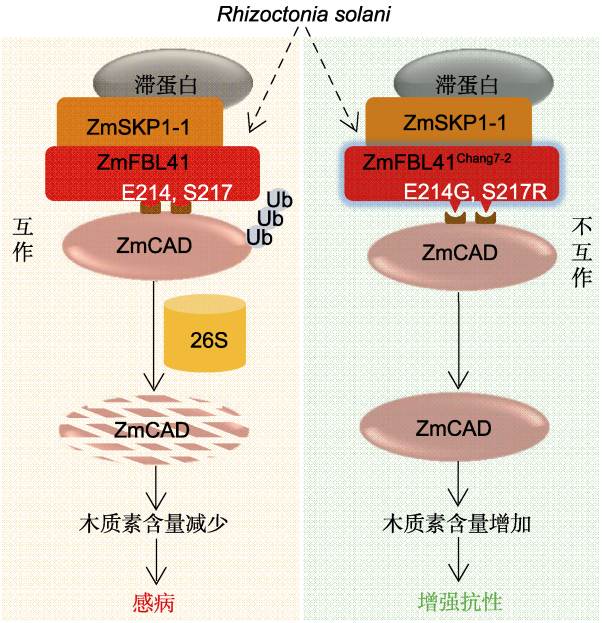

图1 ZmFBL41介导的纹枯病抗性

ZmFBL41与ZmSKP1-1互作形成SCF复合体，通过26S蛋白酶体降解底物ZmCAD，减少木质素的积累，从而使玉米易感纹枯病。而ZmFBL41$^{Chang7\text{-}2}$因其中2个关键氨基酸位点变异(E214G，S217R)，不能结合并降解底物ZmCAD，从而引起木质素积累，使玉米对纹枯病的抗性增强。

Figure 1 A model for ZmFBL41-mediated banded leaf and sheath blight (BLSB) resistance

ZmFBL41 interacts with ZmSKP1-1 to form the SCF complex, and recruits ZmCAD for 26S proteasome-mediated degradation, resulting in reduced lignin synthesis and increased susceptibility of maize to *R. solani*. However, in the natural maize resource Chang7-2, the protein ZmFBL41$^{Chang7\text{-}2}$ with two amino acid variations (E214G and S217R) is not able to interact with ZmCAD, leading to failure in degradation of ZmCAD and resulting in accumulation of lignin, which consequently enhances resistance to *R. solani*.

综上所述，该研究团队发现了SCF复合体对玉米纹枯病抗性的重要调控作用，并率先揭示了SCF复合体可通过降解肉桂醇脱氢酶调控植物免疫反应和抗性的新型分子机制(图1)。

纹枯病致病菌*R. solani*宿主范围广且危害大，挖掘作物的抗性基因并加以育种应用，是有效防控纹枯病危害的重要措施。该研究不仅揭示了玉米和水稻等作物纹枯病抗性调控的重要机制；而且鉴定的系列自然等位变异的抗性资源(如ZmFBL41$^{Chang7\text{-}2}$)，可直接用于抗纹枯病优良玉米新品种的培育，为玉米和水稻等作物抗病育种提供了重要资源和有效途径。

参考文献

Baruah P, Lal S (1981). Hostrange of *Rhizoctonia solani* f. sp. *sasakii*, then incitant of banded sclerotial disease of maize. *Indian Phytopath* **34**, 494–496.

Hooda KS, Khokhar MK, Parmar H, Gogoi R, Joshi D, Sharma SS, Yadav OP (2017). Banded leaf and sheath blight of maize: historical perspectives, current status and future directions. *Proc Natl Acad Sci India Sect B Biol Sci* **87**, 1041–1052.

Li N, Lin B, Wang H, Li X, Yang F, Ding X, Yan J, Chu Z (2019). Natural variation in *ZmFBL41* confers banded leaf and sheath blight resistance in maize. *Nat Genet* **51**, 1540–1548.

Li Z, Pinson SRM, Marchetti MA, Stansel JW, Park WD (1995). Characterization of quantitative trait loci (QTLs) in cultivated rice contributing to field resistance to sheath blight (*Rhizoctonia solani*). *Theor Appl Genet* **91**, 382–388.

Maeda S, Dubouzet JG, Kondou Y, Jikumaru Y, Seo S,

Oda K, Matsui M, Hirochika H, Mori M (2019) The rice CYP78A gene *BSR2* confers resistance to *Rhizoctonia solani* and affects seed size and growth in *Arabidopsis* and rice. *Sci Rep* **9**, 587.

Ogoshi A (1987). Ecology and pathogenicity of anastomosis and interspecific groups of *Rhizoctonia solani* Kuhn. *Ann Rev Phytopathol* **25**, 125–143.

Peng X, Wang H, Jang JC, Xiao T, He H, Jiang D, Tang X (2016). OsWRKY80-OsWRKY4 module as a positive regulatory circuit in rice resistance against *Rhizoctonia solani*. *Rice* **9**, 63.

Richa K, Tiwari IM, Devanna BN, Botella JR, Sharma V, Sharma TR (2017). Novel chitinase gene *LOC_Os 11g47510* from indica rice Tetep provides enhanced resistance against sheath blight pathogen *Rhizoctonia solani* in rice. *Front Plant Sci* **8**, 596.

Sharma RC, Srinivas P, Batsa BK (2002). Banded leaf and sheath blight of maize its epidemiology and management. In: Rajbhandari NP, Ransom JK, Adhikari K, Palmer AFE, eds. Proceedings of a Maize Symposium Held. Kathmandu: NARC and CIMMYT. pp. 108–112.

Sharma RR, Gour HN, Rathore RS (2004). Etiology of banded leaf and sheath blight symptoms on maize. *J Mycol Plant Pathol* **34**, 56–59.

Singh BM, Sharma YR (1976). Evaluation of maize germplasm to banded sclerotial disease and assessment of yield loss. *Indian Phytopath* **29**, 129–132.

Wang H, Meng J, Peng X, Tang X, Zhou P, Xiang J, Deng X (2015). Rice WRKY4 acts as a transcriptional activator mediating defense responses toward *Rhizoctonia solani*, the causing agent of rice sheath blight. *Plant Mol Biol* **89**, 157–171.

Discovery of ZmFBL41$^{Chang7-2}$ as A Key Weapon against Banded Leaf and Sheath Blight Resistance in Maize

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Abstract The fungal pathogen *Rhizoctonia solani* causes banded leaf and sheath blight (BLSB) in maize (*Zea mays*) and sheath blight (ShB) in rice (*Oryza sativa*). *R. solani* has a wide range of host and severely threatens crop production. The lack of resistant resources against BLSB and the poor understanding of disease resistance mechanism hamper the development of effective approaches to control this fungal disease. Recently, Chinese scientists have made a breakthrough discovery that an F-box protein ZmFBL41 mediates the proteasomal degradation of cinnamyl-alcohol dehydrogenase ZmCAD to regulate BLSB and ShB disease resistance. By genome-wide association analysis, *GRMZM2G 109140* (*ZmFBL41*) was identified as a major QTL candidate gene associated with BLSB disease resistance. ZmFBL41 protein is a member of SKP1-Cullin-F-box (SCF) E3 ubiquitin ligase complex which mediates the degradation of ZmCAD, thus reducing the accumulation of lignin and rendering maize more susceptible to *R. solani*. Interestingly, in the maize inbred line Chang7-2, the natural variation on two amino acids in ZmFBL41$^{Chang7-2}$ results in resistance against BLSB. Mechanistically, ZmFBL41$^{Chang7-2}$ fails to interact with and degrade its substrate ZmCAD, leading to the accumulation of lignin, which consequently enhances maize resistance. This study not only discovers a novel molecular mechanism underlying disease resistance of maize against *R. solani*, but also provides important theoretical basis and genetic resources for breeding maize and other crops with improved disease resistance.

Key words plant immunity, SKP1-Cullin-F-box, lignin, banded leaf and sheath blight, maize, rice

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