

2024



年度报告



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一、实验室概况

植物抗逆高效全国重点实验室“坚持面向世界科技前沿、坚持面向经济主战场、坚持面向国家重大需求、坚持面向人民生命健康”，在原植物生理学与生物化学国家重点实验室的基础上，通过吸纳并整合中国农业大学多个国家级和省部级研究平台的优势力量，强化特色，弥补短板，聚焦科学前沿，按照国家重大需求导向，进行优化重组。中国科学院院士娄成后教授、中国科学院院士阎隆飞教授等老一辈科学家在实验室的研究工作积累方面做出了重要贡献。

实验室立足粮食安全和农业可持续发展的国家重大战略需求，聚焦植物逆境生物学基础研究领域的前沿科学问题，以提升主要农作物抗逆性和资源高效利用为主攻方向，开展植物环境适应性的前沿基础研究，解析植物响应与适应逆境胁迫、资源高效利用的生理生化和分子基础，构建并完善植物抗逆高效的基础理论体系；研究作物抗逆高效优异性状形成的遗传基础和分子调控机制，挖掘具有重大育种价值的优异基因，为抗逆高效作物新品种的培育提供基因资源和理论指导。

实验室设 4 个研究方向：（1）植物响应逆境胁迫的生理生化和分子基础；（2）植物养分高效利用的调控网络；（3）植物适应复杂环境可塑性生长的理论基础；（4）作物抗逆高效性状耦合模型的构建。

实验室面向我国重大战略需求和植物科学国际发展前沿，长期持续开展“植物/抗逆高效的生理生化及分子生物学”的创新性、前瞻性和战略性研究，引领该领域的国际学术研究方向，在植物响应非生物逆境胁迫的分子调控机制，植物养分和光能高效利用的基础理论研究，作物环境适应机制解析，作物抗逆高效种质创新，以及作物抗逆高效化学调控技术等方面取得了一系列具有国际影响的研究成果，为我国农业可持续发展和农民增产增收做出了重要贡献。

实验室根据研究方向和工作职能，设置三个研究团队和一个研究技术中心，三个团队包括：植物抗逆研究团队、植物资源高效利用研究团队、作物抗逆高效种质创新研究团队，开放共享的研究技术中心为实验室科研工作提供技术支撑和保障。

实验室首席科学家为中国科学院院士武维华教授，实验室主任为教育部重大人才工程特聘教授杨淑华教授。实验室学术委员会主任为中国科学院院士种康研究员，实验室学术委员会副主任为中国科学院院士曹晓风研究员和中国农业大学巩志忠教授，实验室学术委员会由来自国内外不同专业领域的专家学者组成。



实验室主要学术带头人：武维华、杨淑华、郭岩、巩志忠、李召虎、段留生、傅缨、李大伟、徐明良、郑绍建等。

实验室主要学术骨干：任东涛、毛同林、秦峰、陈益芳、田丰、王毅、杨小红、李继刚、蒋才富、张静、施怡婷、徐凌、周文焜、王献兵、田长富、张永亮、毕国志、宋文、刘建祥、徐娟、杨光辉等。

实验室力争建设成为国际一流的植物抗逆高效理论创新高地、作物稳产高产种质创新研发基地、植物学和作物学顶尖人才培养基地、植物逆境生物学国际合作交流中心，为保障国家粮食安全和农业绿色可持续发展提供重要科技支撑。

本实验室现有固定人员 70 人，其中中科院院士 1 人、教育部重大人才工程特聘教授 8 人、教育部重大人才工程青年学者 4 人、国家“杰出青年科学基金”获得者 20 人，国家/海外“优秀青年科学基金”获得者 15 人，青年创新人才 4 人。国家自然科学基金创新研究群体 1 个，等。在 70 位固定人员中包括教授 47 人、副教授 18 人、中级研究人员和科研辅助人员 5 人，其中专职或兼职的实验技术平台管理人员 10 人。

2024 年有三位年轻科研人员分别获得国家基金委杰出青年基金、优秀青年基金、海外优秀青年基金。

2024 年度实验室执行各类研究项目 146 项，包括国家自然科学基金委创新研究群体 1 项，国家自然科学基金杰出青年基金 6 项、优秀青年基金 4 项、重点项目 11 项、国际（地区）合作与交流项目 4 项、面上项目 36 项、青年项目 8 项、联合基金项目 3 项；科技部国家重点研发计划（含子课题及青年科学家项目）30 项，政府间国际科技创新合作项目 2 项，科技创新 2030 项目 2 项；农业农村部农业生物育种国家科技重大专项（含子课题）9 项，NYGG 项目 4 项；其它项目 26 项，经费合计 6560.935 万元。

2024 年度实验室固定人员在被 SCI 收录的期刊上发表重要研究论文 78 篇，其中 *Nature* 2 篇，*Nat Genet* 2 篇，*Cell Res* 1 篇，*Trends Plant Sci* 1 篇，*Mol Plant* 4 篇，*Nat Plants* 2 篇，*Trends Microbiol* 1 篇，*Nat Commun* 3 篇，*Sci Bull* 2 篇，*Annu Rev Genet* 1 篇，*Plant Biotechnol J* 3 篇，*Genom Proteom Bioinf* 1 篇，*Plant Cell* 4 篇，*New Phytol* 6 篇，*Curr Biol* 1 篇，*Plant Commun* 2 篇，*J Integr Plant Biol* 9 篇，*Cell Rep* 2 篇，*Curr Opin Plant Biol* 1 篇，*Plant Physiol* 4 篇。累计 SCI 影响因子 944.5，平均影响因子 12.11/篇。2024 年度实验室获得发明专利和软件著作权 22 项。

2024 年 8 月 5-8 日实验室举办了“2024 植物逆境应答与环境适应性学术研讨会



（2024 International Symposium on Plant Environmental Resilience）”。会议邀请了来自德国、加拿大、韩国、日本、中国等 5 个国家国际植物逆境生物学领域的知名科学家介绍本领域最新研究进展，并深入讨论开展植物逆境信号转导、植物响应逆境分子机制等方面的国际合作。会议外方专家 9 人，中方专家 19 人，会议期间共有约 500 人参会。2024 年 11 月 4-9 日实验室举办了“中以植物与环境互作双边研讨会”，以方专家 11 人和中方专家 14 人分别做了学术报告，展示最新研究进展，深入探讨交流与合作，参会人员 500 余人。

2024 年实验室学术交流活动 229 人次，其中邀请国内外同行来实验室讲学 72 人次，实验室人员在国内外参加会议并报告 90 人次，实验室人员在国内外讲学 67 人次。实验室组织“研究生系列报告”15 次，有 45 位博士研究生做了报告。

2024 年实验室培养研究生共 504 人，直博生和博士生 418 人，硕士生 86 人，博士毕业 20 人，硕士毕业 8 人，2024 年实验室有博士后、客座人员 39 人。



植物抗逆高效全国重点实验室 (SKLPER)

State Key Laboratory of Plant Environmental Resilience

<http://sklper.cau.edu.cn/>

二、实验室管理委员会

序号	管委 会 职 务	姓名	工作单位	职务/职称
1	主 任	孙其信	中国农业大学	校长
2	副主任	田见晖	中国农业大学	副校长
3	副主任	杨淑华	中国农业大学	实验室主任
4	委 员	崔振岭	中国农业大学	科研院常务副院长
5	委 员	陈英义	中国农业大学	科研院基地管理处处长
6	委 员	曲瑛德	中国农业大学	校长助理/发展规划处处长
7	委 员	张永生	中国农业大学	校长助理/后勤处处长
8	委 员	张树彦	中国农业大学	财务处处长
9	委 员	果雅静	中国农业大学	国资处处长
10	委 员	马国玉	中国农业大学	实验室管理处处长
11	委 员	汪九林	中国农业大学	基建处处长
12	委 员	郭 岩	中国农业大学	生物学院院长/实验室副主任
13	委 员	王 毅	中国农业大学	实验室副主任
14	委 员	巩志忠	中国农业大学	教授



植物抗逆高效全国重点实验室 (SKLPER)
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三、实验室学术委员会

序号	姓名	职称	职务	单位	研究方向
1	种 康	研究员/院士	主 任	中国科学院 植物研究所	分子发育生物学
2	曹晓风	研究员/院士	副主任	中国科学院遗传与 发育生物学研究所	植物遗传与生物化学
3	巩志忠	教 授	副主任	中国农业大学	植物逆境生物学
4	林鸿宣	研究员/院士	委 员	中国科学院 分子植物科学 卓越创新中心	作物遗传育种
5	朱健康	教授/院士 (美国)	委 员	南方科技大学	植物逆境生物学
6	万建民	研究员/院士	委 员	中国农业科学院 作物科学研究所	作物遗传与分子生物学
7	钱 前	研究员/院士	委 员	中国农业科学院 作物科学研究所	作物遗传育种
8	康振生	教授/院士	委 员	西北农林科技大学	植物病理学
9	薛勇彪	研究员	委 员	中国科学院 北京基因组研究所	植物遗传与分子生物学
10	瞿礼嘉	教 授	委 员	北京大学	植物发育生物学
11	宋纯鹏	教 授	委 员	河南大学	植物逆境生物学
12	戚益军	教 授	委 员	清华大学	植物表观遗传学
13	李召虎	教 授	委 员	中国农业大学	作物抗逆高效化控生理
14	李建生	教 授	委 员	中国农业大学	玉米遗传育种
15	赖锦盛	教 授	委 员	中国农业大学	玉米遗传育种
16	郭 岩	教 授	委 员	中国农业大学	植物逆境生物学
17	杨淑华	教 授	委 员	中国农业大学	植物逆境生物学
18	王 毅	教 授	学 术 秘 书	中国农业大学	植物养分高效



四、2024年学术委员会会议纪要

时 间

2025 年 1 月 21 日 (星期二) 9:00-12:00

地 点

中国农业大学 生命科学研究 第七会议室 (4057 室)



五、重要成果简介

（一）植物/作物抗逆的生理生化及分子生物学基础

在植物响应干旱胁迫研究方面，阐明了 ZmCPK2 和 ZmCPK17 调控玉米响应干旱胁迫的分子机制（Hu et al., *J Integr Plant Biol*, 巩志忠课题组）；阐释了 ZmSnRK2.2 通过磷酸化 ZmAL14 调控玉米耐旱的机理（Wang et al., *J Integr Plant Biol*, 王瑜课题组）；揭示了 ZmMIK2-ZmC2DP1 负调控玉米抵抗盐胁迫和干旱胁迫的分子机制（Yang et al., *J Genet Genomics*, 秦峰课题组）；阐释了 ZmCRK1 调控质膜 H⁺-ATPase 响应玉米干旱胁迫的机制（Liu et al., *New Phytol*, 陈丽梅课题组）。

在植物响应盐胁迫研究方面，揭示了液泡动态变化调控植物耐盐性的分子机制（Liu et al., *Plant Cell*, 郭岩课题组）；阐明了 JA 信号通路在植物响应盐胁迫中的分子机制（Li et al., *Cell Rep*, 傅缨课题组）；阐明了 OsHKT1;1 和 OsHKT2;1 的结构，从结构层面解析了水稻阳离子转运体 HKTs 在盐胁迫下的作用（Gao et al., *J Integr Plant Biol*, 杨光辉课题组）；概述了目前植物耐盐分子机理的研究进展（Liang et al., *J Integr Plant Biol*, 蒋才富课题组）。

在植物抵抗温度胁迫（高温和低温）方面，揭示了玉米耐低温基因 *HSF21* 通过维持玉米低温胁迫下脂代谢稳态正调控玉米耐冷性的分子机理（Gao et al., *Mol Plant*, 杨淑华课题组）；阐明了两类激酶对钙离子通道 CNGC20 不同位点的磷酸化，实现对通道活性和蛋白稳定性的调节，从而精细调控植物低温应答的分子机制（Peng et al., *Plant Cell*, 杨淑华课题组）；通过不同的角度系统总结植物在低温胁迫条件下生存和生长的机制（Ding et al., *Annu Rev Genet*, 丁杨林、杨淑华课题组）。揭示了水稻高温抗性的昼夜差异调控机制（Yang et al., *Sci Bull*, 刘建祥课题组）；分别阐明了 NFXL1 和 XBAT31 调控拟南芥生殖期高温胁迫抗性的分子机制（Zhu et al., *J Integr Plant Biol*; Zhang et al., *Cell Rep*, 刘建祥课题组）；揭示了 CCaP1/CCaP2/CCaP3 蛋白介导高温下植物生长的作用机理（Wang et al., *Plant Commun*, 刘建祥课题组）。

在植物抗病方面，首次揭示了 TIR 结构域作为最小免疫模块通过形成凝聚体激活的新模式（Song et al., *Nature*, 宋文课题组）；揭示了 CRP 蛋白促进病毒粒子形态建成的新功能（Yue et al., *PLoS Pathog*, 李大伟课题组）；揭示了植物弹状病毒编码的孔蛋白 P9 促进昆虫传毒的分子机理（Gao et al., *Plant Cell*, 王献兵课题组）；揭示了 SGT1 的



分子调控网络，并揭示了一个新的协调植物先天免疫的信号转导模块 SGT1-NSL1 (Zhang et al., *Mol Plant*, 张永亮课题组); 鉴定了 RNAi 通路的一个潜在新组 RH20 通过与 SGS3/RDR6 bodies 互作正调控 RNAi 介导的抗病毒免疫的分子机制 (Wen et al., *Plant Biotechnol J*, 张永亮课题组); 揭示了玉米 WAK-SnRK1 α 2-WRKY 分子模块通过调控养分可利用性来抵御丝黑穗病的分子机制 (Zhang et al., *Mol Plant*, 徐明良课题组)。

(二) 植物/作物水分、养分和光高效利用的分子生理学机制

在植物水分高效利用方面，揭示了 SNARE 蛋白的磷酸化是植物调控 SNARE 复合体组装和膜融合的重要策略，确定了 LKS4/SGN1 通过磷酸化 SYP121，在光诱导的气孔开启中发挥关键作用 (Ding et al., *Curr Biol*, 傅纛课题组); 发现了玉米 ZmPHR1 协同调控磷素利用和水分胁迫的分子机制，为挖掘调控玉米营养高效和环境广适的关键基因提供了新思路 (Tian et al., *Plant Biotechnol J*, 武维华、陈益芳课题组)。

在植物养分高效利用研究方面，阐释了真核生物中 InsP6 生物合成的功能机制，以及 InsP6 介导细胞外磷信号调控胞内磷稳态的作用机制 (Xu et al., *Nat Commun*, 郑绍建、丁忠杰课题组); 解析了植物从铝离子感知到下游抗铝反应启动的完整信号通路，为生物体的离子感知机制提供了新的见解 (Ding et al., *Cell Res*, 郑绍建课题组); 发现了类受体激酶 WAKL4-NRAMP1 调控模块介导的植物主动降低镉累积的新机制 (Yuan et al., *Nat Commun*, 郑绍建课题组); 发现了 CPK28 介导的磷酸化增强了 NRT2.1 在氮剥夺过程中的硝酸盐转运活性 (Yue et al., *New Phytol*, 武维华、汪洋课题组); 解析了光信号调控植物氮、钾养分根冠转运的分子机制，确定了一个驱动水分和养分根冠运输的分子开关 (Jing et al., *New Phytol*, 武维华、王毅课题组); 阐明了 EIN3/EILs-ERF9-HAK5 模块调控乙烯介导的钾离子吸收的分子机制 (Xiao et al., *New Phytol*, 李召虎、田晓莉课题组); 综述了水稻根感知环境磷水平及根构型响应磷水平的分子机制研究进展，讨论了水稻养分高效根构型遗传改良的实践策略 (Lu et al. *Mol Plant*; Lu et al. *Plant Physiol*, 毛传澡课题组)。

在生物固氮研究方面，概述了“根际氮浓度-根瘤细胞内金属离子浓度-功能性根瘤”的分子调控模式，及其在现代农业高效固氮豆科植物改良中的巨大潜力 (Qiao et al., *Nat Plants*, 梁鹏博课题组); 综述了几丁质介导的大豆根际共生菌和孢囊线虫的拮抗分子机制 (Zhang et al., *Trends Microbiol*, 梁鹏博课题组)。



在植物光高效利用研究方面，鉴定了一类能够磷酸化 phyA 的蛋白激酶 PPKs，并且阐明了 TZP 通过液-液相分离促进 PPKs 磷酸化 phyA 的分子机制，为进一步深入解析远红光信号途径以及光信号调控网络提供了新的见解（Feng et al., *Nat Plants*, 李继刚课题组）；揭示了 ABI4 与 PIF4 组成的分子模块在调控 CRYs 介导的蓝光信号途径中发挥重要作用（Song et al., *J Integr Plant Biol*, 李继刚课题组）。

（三）植物/作物复杂环境下的生长可塑性调控机理

在植物生长发育研究方面，发现了 ZmGDI α -hel 通过调控赤霉素活性，进而调控玉米粗缩病隐性数量抗性的机理（Deng et al., *Nat Commun*, 徐明良课题组）；解析了冠菌素通过介导茉莉酸和油菜素内酯信号途径，调控玉米节间伸长的分子机制（Wang et al., *Plant Physiol*, 段留生、周于毅课题组）；揭示了 ECAP-LUG-BEH3 复合体通过对 SPL 基因的表现遗传调控，进而特异调控小孢子母细胞发生的分子机制（Shi et al., *Plant Cell*, 傅纛课题组）；解析了拟南芥微管生长驱动的囊泡运输参与保卫细胞质膜上离子通道的再分布，从而调控气孔运动的分子机理（Zhong et al., *Nat Commun*, 傅纛课题组）；从环境因子、氧化还原调控、生物胁迫和非生物胁迫等四个方面，综述了植物分生组织中干细胞胁迫应答的分子机制（Zeng et al., *Curr Opin Plant Biol*, 周文焜课题组）；揭示了转录因子 MYB52 负调控微丝结合蛋白 ADF9 介导的微丝成束，进而调节铺板细胞形态建成的分子机制（Qiu et al., *J Integr Plant Biol*, 毛同林、王向锋课题组）。

发现了 LRH-RSL4 反馈调节环调控根毛有限生长的分子机制，为根毛的有限生长机制提供了新的见解（Cui et al., *Curr Biol*, 郑绍建课题组）；建立了一个条件型失活 *mpk4* 突变体研究体系，对 MPK4 在植物生长/发育和免疫过程中的功能提出了新见解（Zhang et al., *Plant Physiol*, 徐娟课题组）；揭示了 SNARE 蛋白介导水稻中生长素转运体的胞内转运及根系形态建成（Zhu et al., *New Phytol*, 毛传澡课题组）；发现了酰基载体蛋白硫酯酶 GmFATA1 和 GmFATA2 调控大豆脂肪酸积累和生长发育的分子机理（Liao et al., *Plant J*, 寿惠霞课题组）。

（四）作物抗逆高效的分子设计和种质创新

在作物抗逆基因挖掘方面，建立了 *TIP4;3* 基因表达水平与玉米耐冷性之间的联系，揭示了 *TIP4;3* 调控玉米耐冷性的分子机制（Zeng et al., *Plant Biotechnol J*, 施怡婷、



杨淑华课题组); 利用全基因组关联分析, 发现了玉米耐低温基因 *HSF21*, 解析了 *HSF21* 正调控玉米耐冷性的分子机制 (Gao et al., *Mol Plant*, 施怡婷、杨淑华课题组); 图位克隆了玉米抗灰斑病主效基因 *ZmWAKL*, 解析了 *ZmWAKL* 正向调控玉米对灰斑病抗性的分子机制 (Zhong et al., *Nat Genet*, 徐明良课题组); 通过图位克隆鉴定了同时对灰斑病、大斑病和小斑病具有广谱抗性的基因 *ZmCPK39*, 解析了 *ZmCPK39* 调控玉米抗病的分子机制 (Zhu et al., *Nat Genet*, 徐明良课题组)。

在作物高产基因发掘方面, 发现了调控玉米株型特征的关键基因 *lac1*, 能够调控玉米群体光合能力, 显著提高玉米密植群体产量, 揭示了玉米智慧株型的调控机制 (Tian et al., *Nature*, 田丰、李继刚课题组); 克隆了调控玉米种子类胡萝卜素合成相关基因 *ZmPTOX*, 系统地解析了玉米类籽粒胡萝卜素变异的遗传机制 (Yin et al., *Plant Biotechnol J*, 杨小红课题组)。

在作物种质创新技术体系建设方面, 构建了新型引导编辑器 PE6c (Cao et al., *J Integr Plant Biol*, 陈其军课题组)。搭建了一个综合性的大豆多组学数据库 SoyOD, 整合了基因组、转录组和群体遗传信息 (Li et al., *Genom Proteom Bioinf*, 寿惠霞课题组)。



六、发表的重要研究论文

序号	通讯 (第一) 作者	论文名称	期刊名称	影响因子
1	田 丰 李继刚	Maize smart-canopy architecture enhances yield at high densities	<i>Nature</i>	54.4
2	宋 文	Substrate-induced condensation activates plant TIR domain proteins	<i>Nature</i>	54.4
3	徐明良	The ZmWAKL-ZmWIK-ZmBLK1-ZmRBOH4 module provides quantitative resistance to gray leaf spot in maize	<i>Nat Genet</i>	36.6
4	徐明良	The ZmCPK39-ZmDi19-ZmPR10 immune module regulates quantitative resistance to multiple foliar diseases in maize	<i>Nat Genet</i>	36.6
5	郑绍建	The LRR receptor-like kinase ALR1 is a plant aluminum ion sensor	<i>Cell Res</i>	36.5
6	任东涛 陈艳梅	Capturing the phosphorylation-linked protein-complex landscape in plants	<i>Trends Plant Sci</i>	22.5
7	毛传澡	New mechanistic insights into phosphate-starvation-regulated plant architecture change and nutrient uptake	<i>Mol Plant</i>	21.4
8	杨淑华 施怡婷	Genetic variation in a heat shock transcription factor modulates cold tolerance in maize	<i>Mol Plant</i>	21.4
9	张永亮	Proximate profiling reveals a conserved SGT1-NSL1 signaling module that activates NLR-mediated immunity	<i>Mol Plant</i>	21.4
10	徐明良	A maize WAK-SnRK1α2-WRKY module regulates nutrient availability to defend against head smut disease	<i>Mol Plant</i>	21.4
11	李继刚	Liquid-liquid phase separation of TZP promotes PPK-mediated phosphorylation of the phytochrome A photoreceptor	<i>Nat Plants</i>	17.1
12	梁鹏博	Zinc sensing in nodules regulates symbiotic nitrogen fixation	<i>Nat Plants</i>	17.1
13	梁鹏博	Chitinase-assisted winner: nematodes antagonize symbiotic microbes	<i>Trends Microbiol</i>	17
14	郑绍建	A clade of receptor-like cytoplasmic kinases and 14-3-3 proteins coordinate inositol hexaphosphate accumulation	<i>Nat Commun</i>	16.1
15	徐明良	ZmGDIα-hel counters the RBSDV-induced reduction of active gibberellins to alleviate maize rough dwarf virus disease	<i>Nat Commun</i>	16.1
16	傅 纓	Endomembrane trafficking driven by microtubule growth regulates stomatal movement in <i>Arabidopsis</i>	<i>Nat Commun</i>	16.1
17	刘建祥	Diurnal regulation of alternative splicing associated with thermotolerance in rice by two glycine-rich RNA-binding proteins	<i>Sci Bull</i>	15.9
18	刘建祥	3D chromatin reorganization during stress responses in plants	<i>Sci Bull</i>	15.9
19	杨淑华 丁杨林 施怡婷	Regulatory networks underlying plant responses and adaptation to cold stress	<i>Annu Rev Genet</i>	14.8



序号	通讯 (第一) 作者	论文名称	期刊名称	影响因子
20	杨小红	Linkage and association mapping in multi-parental populations reveal the genetic basis of carotenoid variation in maize kernels	<i>Plant Biotechnol J</i>	11.6
21	陈益芳	ZmPHR1 contributes to drought resistance by modulating phosphate homeostasis in maize	<i>Plant Biotechnol J</i>	11.6
22	施怡婷	Genetic variation in the aquaporin TONOPLAST INTRINSIC PROTEIN 4;3 modulates maize cold tolerance	<i>Plant Biotechnol J</i>	11.6
23	寿惠霞	SoyOD: An Integrated Soybean Multi-omics Database for Mining Genes and Biological Research	<i>Genom Proteom Bioinf</i>	11.5
24	杨淑华	Differential phosphorylation of CNGC20 antagonistically modulates calcium-mediated freezing tolerance in <i>Arabidopsis</i>	<i>Plant Cell</i>	11.1
25	王献兵	The plant rhabdovirus viroporin P9 facilitates insect-mediated virus transmission in barley	<i>Plant Cell</i>	11.1
26	傅 纓	The adaptor protein ECAP, the co-repressor LEUNIG, and the transcription factor BEH3 interact and regulate microsporocyte generation in <i>Arabidopsis</i>	<i>Plant Cell</i>	11.1
27	王良省	EXECUTER1 and singlet oxygen signaling: A reassessment of nuclear activity	<i>Plant Cell</i>	11.1
28	李召虎 田晓莉	The EIN3/EIL-ERF9-HAK5 transcriptional cascade positively regulates high-affinity K ⁺ uptake in <i>Gossypium hirsutum</i>	<i>New Phytol</i>	10.2
29	陈丽梅	ZmCRK1 negatively regulates maize's response to drought stress by phosphorylating plasma membrane H ⁺ -ATPase ZmMHA2	<i>New Phytol</i>	10.2
30	张永亮	Orchestrating ROS regulation: coordinated post-translational modification switches in NADPH oxidases	<i>New Phytol</i>	10.2
31	汪 洋	CPK28-mediated phosphorylation enhances nitrate transport activity of NRT2.1 during nitrogen deprivation	<i>New Phytol</i>	10.2
32	王 毅	Alternating inverse modulation of xylem K ⁺ /NO ³⁻ loading by HY5 and PIF facilitates diurnal regulation of root-to-shoot water and nutrient transport	<i>New Phytol</i>	10.2
33	毛传澡	The t-SNARE protein OsSYP132 is required for vesicle fusion and root morphogenesis in rice	<i>New Phytol</i>	10.2
34	傅 纓	LKS4-mediated SYP121 phosphorylation participates in light-induced stomatal opening in <i>Arabidopsis</i>	<i>Curr Biol</i>	9.8
35	杨光辉	Structural changes in the conversion of an <i>Arabidopsis</i> outward-rectifying K ⁺ channel into an inward-rectifying channel	<i>Plant Commun</i>	9.4
36	刘建祥	CCaP1/CCaP2/CCaP3 interact with plasma membrane H ⁺ -ATPases and promote thermo-responsive growth by regulating cell wall modification in <i>Arabidopsis</i>	<i>Plant Commun</i>	9.4



序号	通讯 (第一) 作者	论文名称	期刊名称	影响因子
37	于静娟	The m ⁶ A reader SiYTH1 enhances drought tolerance by affecting the messenger RNA stability of genes related to stomatal closure and reactive oxygen species scavenging in <i>Setaria italica</i>	<i>J Integr Plant Biol</i>	9.3
38	刘建祥	NFXL1 functions as a transcriptional activator required for thermotolerance at reproductive stage in <i>Arabidopsis</i>	<i>J Integr Plant Biol</i>	9.3
39	杨光辉	Structural insights into the <i>Oryza sativa</i> cation transporters HKTs in salt tolerance	<i>J Integr Plant Biol</i>	9.3
40	郭 岩 杨永青 蒋才富	Designing salt stress-resilient crops: Current progress and future challenges	<i>J Integr Plant Biol</i>	9.3
41	陈其军	PE6c greatly enhances prime editing in transgenic rice plants	<i>J Integr Plant Biol</i>	9.3
42	巩志忠	Ca ²⁺ -independent ZmCPK2 is inhibited by Ca ²⁺ -dependent ZmCPK17 during drought response in maize	<i>J Integr Plant Biol</i>	9.3
43	王 瑜	Phosphorylation of ZmAL14 by ZmSnRK2.2 regulates drought resistance through derepressing ZmROP8 expression	<i>J Integr Plant Biol</i>	9.3
44	郑绍建	STOP1 regulates CCX1-mediated Ca ²⁺ homeostasis for plant adaptation to Ca ²⁺ deprivation	<i>J Integr Plant Biol</i>	9.3
45	李继刚	Regulation of cryptochrome-mediated blue light signaling by the ABI4-PIF4 module	<i>J Integr Plant Biol</i>	9.3
46	傅 缨 李长江	Jasmonate signaling pathway confers salt tolerance through a NUCLEAR FACTOR-Y trimeric transcription factor complex in <i>Arabidopsis</i>	<i>Cell Rep</i>	8.5
47	刘建祥	XBAT31 regulates reproductive thermotolerance through controlling the accumulation of HSFB2a/B2b under heat stress conditions	<i>Cell Rep</i>	8.5
48	周文焜	Tipping the balance: The dynamics of stem cell maintenance and stress responses in plant meristems	<i>Curr Opin Plant Biol</i>	8.3
49	徐 娟	Chemical-sensitized MITOGEN-ACTIVATED PROTEIN KINASE 4 provides insights into its functions in plant growth and immunity	<i>Plant Physiol</i>	7.6
50	毛传澡	Developmental responses of roots to limited phosphate availability: Research progress and application in cereals	<i>Plant Physiol</i>	7.6
51	李继刚	Molecular characterization and functional analyses of maize phytochrome A photoreceptors	<i>Plant Physiol</i>	7.6
52	段留生 周于毅	Jasmonate mimic modulates cell elongation by regulating antagonistic bHLH transcription factors via brassinosteroid signaling	<i>Plant Physiol</i>	7.6
53	刘建祥	Regulation of metal homeostasis by two F-group bZIP transcription factors bZIP48 and bZIP50 in rice	<i>Plant Cell Environ</i>	7.6



序号	通讯 (第一) 作者	论文名称	期刊名称	影响因子
54	李继刚 马 亮	Molecular mechanisms underlying coordinated responses of plants to shade and environmental stresses	<i>Plant J</i>	7.1
55	寿惠霞	The acyl-acyl carrier protein thioesterases GmFATA1 and GmFATA2 are essential for fatty acid accumulation and growth in soybean	<i>Plant J</i>	7.1
56	周于毅 段留生	ZmSCE1a positively regulates drought tolerance by enhancing the stability of ZmGCN5	<i>Plant J</i>	7.1
57	田晓莉	Effect of different irrigation and fertilizer coupling on the liquiritin contents of the licorice in Xinjiang arid area	<i>Ecol Indic</i>	7
58	李景睿	The SALT OVERLY SENSITIVE 2–CONSTITUTIVE TRIPLE RESPONSE1 module coordinates plant growth and salt tolerance in <i>Arabidopsis</i>	<i>J Exp Bot</i>	6.8
59	段留生 周于毅	Triacontanol delivery by nano star shaped polymer promoted growth in maize	<i>Plant Physiol Bioch</i>	6.2
60	段留生 周于毅	Unveiling the regulatory role of miRNAs in internode elongation: integrated analysis of microRNA and mRNA expression profiles across diverse dwarfing treatments in maize	<i>J Agric Food Chem</i>	6
61	段留生	Design, synthesis, and bioactivities of N-heterocyclic ureas as strigolactone response antagonists against parasitic-weed seed germination	<i>J Agric Food Chem</i>	6
62	郭 岩	Insights into plant salt stress signaling and tolerance	<i>J Genet Genomics</i>	5.8
63	秦 峰	An LRR-RLK protein modulates drought- and salt-stress responses in maize	<i>J Genet Genomics</i>	5.8
64	施怡婷	Genetic and lipidomic analyses reveal the key role of lipid metabolism for cold tolerance in maize	<i>J Genet Genomics</i>	5.8
65	陈益芳	Phosphorus acquisition, translocation, and redistribution in maize	<i>J Genet Genomics</i>	5.8
66	段留生	Design, synthesis and biological evaluation of novel phenyl-substituted naphthoic acid ethyl ester derivatives as strigolactone receptor inhibitor	<i>Int J Mol Sci</i>	5.6
67	张明才 李召虎	Ethylene accelerates maize leaf senescence in response to nitrogen deficiency by regulating chlorophyll metabolism and autophagy	<i>Crop J</i>	5.6
68	徐明良	Multi-omics analysis reveals the pivotal role of phytohormone homeostasis in regulating maize grain water content	<i>Crop J</i>	5.6
69	寿惠霞	Role of OsbHLH156-OsIRO2 transcription factor complex in regulating manganese, copper and zinc transporters in rice	<i>J Exp Bot</i>	5.6
70	寿惠霞	PHO1: linking phosphate nutrition translocation and floral signalling in plants	<i>J Exp Bot</i>	5.6



序号	通讯 (第一) 作者	论文名称	期刊名称	影响因子
71	李大伟	Zn ²⁺ -dependent association of cysteine-rich protein with virion orchestrates morphogenesis of rod-shaped viruses	<i>PLoS Pathog</i>	5.5
72	苏 震	Nuclear lamina component KAKU4 regulates chromatin states and transcriptional regulation in the <i>Arabidopsis</i> genome	<i>BMC Biol</i>	5.4
73	苏 震	KAKU4 regulates leaf senescence through modulation of H3K27me3 deposition in the <i>Arabidopsis</i> genome	<i>BMC Plant Biol</i>	5.2
74	毛传澡	Protein phosphatase 5 mediates plant growth and phosphate homeostasis in rice	<i>Environ Exp Bot</i>	5.2
75	任东涛	Identification of the fructose 1,6-bisphosphate aldolase (FBA) family genes in maize and analysis of the phosphorylation regulation of ZmFBA8	<i>Plant Sci</i>	4.9
76	段留生	Deciphering physiological and transcriptional mechanisms of maize seed germination	<i>Plant Mol Biol</i>	4.6
77	徐明良	The maize ZmCPK39-ZmKnox2 module regulates plant height	<i>aBIOTECH</i>	4.5
78	陈其军	Enhanced editing efficiency in <i>Arabidopsis</i> with a LbCas12a variant harboring D156R and E795L mutations	<i>aBIOTECH</i>	4.5

累计 **SCI** 影响因子 **944.5**，平均影响因子 **12.11/每篇**。

七、获得的发明专利和软件著作权

序号	成果名称	所有完成人员排名	专利号 软件登记号	授权 公告日
1	一种提高大豆种子含油量的方法	寿惠霞，廖文英，郭润泽	ZL202210311249.9	2024.01.05
2	一种玉米耐高温评价的方法	张帅松，陈丽梅，李建生，贾冬云	ZL202310592286.6	2024.02.20
3	玉米灰斑病抗性相关蛋白及其编码基因与应用	徐明良，钟涛，朱芒，郭晨煜，房正，张晓辉	ZL202210012417.4	2024.02.20
4	具有独脚金内酯活性的苯乙酯烯醚内酯类化合物及其制备与应用	段留生，王春英，于春欣，赵汗青，郭兵博，杜琳，王兴，周于毅，姜峰，李召虎，谭伟明	ZL202210696963.4	2024.03.06
5	ZmMAPK 蛋白及其编码基因在调控植物低温胁迫耐性中的应用	施怡婷，杨淑华，李卓洋	ZL202011565861.6	2024.03.19
6	灰斑病抗性相关蛋白 ZmWAK-RLK 及其编码基因和应用	徐明良，钟涛，潘兴明，朱芒，张艳，徐凌，刘丽	ZL202080013982.1	2024.03.26
7	一种多用途微小物夹取镊	梁鹏博，曾梓健，刘倩，乔李锦	ZL202322400075.6	2024.04.02
8	一种提高先导编辑效率的载体和方法	陈其军，柴一萍，姜媛媛	ZL202110812557.5	2024.04.16
9	一种棉花脱叶组合物及采用其的棉花脱叶方法	田晓莉，廖宝鹏，魏泽欣，李芳军，杜明伟，李召虎	ZL202310031890.1	2024.06.07
10	一种新型基因编辑系统及相关载体和方法	陈其军，姜媛媛，柴一萍	ZL202110812232.7	2024.06.21
11	矮 20 蛋白、其编码基因及应用	王喜庆，赵晓明，庄军红，陈丽梅	ZL202110324876.1	2024.06.21
12	一种玉米抗倒伏基因及其相关蛋白和生物材料的应用	王毅，武维华，姬赆，韩武，王喜庆，陈丽梅，赵晓明	ZL202310720864.X	2024.06.28
13	一种耐受氯离子毒害的玉米抗盐 QTL 基因及其应用	蒋才富，尹攀，张敬波	ZL202310232675.4	2024.10.22
14	一种玉米氮高效利用基因及其分子标记和应用	张静，贾冠南，陈国经纬	ZL202211562186.0	2024.10.22
15	水稻根形态建成调控基因 CLRD1 及其应用	毛传澡，朱建树，李梦真，徐纪明，吴运荣，莫肖蓉	ZL202210683006.8	2024.11.06
16	一个玉米氮利用相关基因 ZNCRG2 及其应用	张静，赵雪米，王亚平	ZL202211671933.4	2024.11.08



序号	成果名称	所有完成人员排名	专利号 软件登记号	授权 公告日
17	ROOT-SECRETED PEPTIDE PEP1 IN RICE AND GENE ENCODING THE SAME AND USE THEREOF	毛传澡，蒙福宁，向丹，王奥迪	US 17, 180, 930	2024.03.29
18	ZMWAK-RLK PROTEIN RELATED TO GRAY LEAF SPOT RESISTANCE, AND ENCODING GENE AND APPLICATION THEREOF-US	徐明良，钟涛，潘兴明，朱芒，张艳，徐凌，刘丽	US 12, 077, 769 B2	2024.09.03
19	基于激光雷达智能识别算法的田间作物株数检测软件 V1.0	王耀君，杨知予，夏婉可，王喜庆	2024SR0634616	2024.05.11
20	基于知识检索增强的私域文件问答助手软件 V1.0	陈建，焦文池，杨晨光，王喜庆，张帅松，谢朋洋	2024SR1593093	2024.10.23
21	面向多需求的生物数据处理软件 V1.0	林海波，李奕则，闫宇涵，吴瑞明，李龙飞，查东辉，王文飞，黄铭，王喜庆，马晓栋	2024SR1711525	2024.11.06
22	自适应可视多平台主成分分析软件 [简称：多平台主成分分析软件] V1.0	马晓栋，闫宇涵，李奕则，李龙飞，吴瑞明，查东辉，黄铭，王文飞，王喜庆，林海波	2024SR1708999	2024.11.06

八、承担的主要研究项目

序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
1	郭 岩	植物非生物胁迫感受和应答	31921001	国家自然科学基金创新群体
2	王 毅	植物感受低钾胁迫的分子机理	32025004	国家自然科学基金杰出青年项目
3	田 丰	玉米驯化与适应的分子遗传基础	32025027	国家自然科学基金杰出青年项目
4	李继刚	植物光信号转导	32225006	国家自然科学基金杰出青年项目
5	杨小红	玉米重要产量与品质性状的遗传基础	32225036	国家自然科学基金杰出青年项目
6	蒋才富	作物抗逆生理	32325037	国家自然科学基金杰出青年项目
7	王献兵	植物病毒病害	32425046	国家自然科学基金杰出青年项目
8	张永亮	植物病毒学	32122070	国家自然科学基金优秀青年项目
9	毕国志	植物免疫信号转导	32322008	国家自然科学基金优秀青年项目
10	杨光辉	植物响应逆境胁迫中离子浓度稳态的调节	32422038	国家自然科学基金优秀青年项目
11	宋 文	植物抗病蛋白激活免疫的分子机制		国家自然科学基金优秀青年项目（海外）
12	李召虎	棉花化控栽培分子机制及轻简作物构建研究	31930079	国家自然科学基金重点项目
13	徐明良	玉米细胞壁相关激酶 ZmWAK 介导的丝黑穗病数量抗性分子机理	31930082	国家自然科学基金重点项目
14	巩志忠	钙信号调控玉米抗旱的分子机制研究	32030008	国家自然科学基金重点项目
15	郭 岩	盐胁迫下植物根系生长发育调控的分子机制	32130007	国家自然科学基金重点项目
16	杨淑华	转录因子 CBFs 在转录后水平调控植物响应低温胁迫的分子机制	32230005	国家自然科学基金重点项目
17	傅 纓	被子植物小孢子母细胞发生的调控机制研究	32230030	国家自然科学基金重点项目
18	毛同林	微管骨架参与植物侧根发育的生物学机制	32330028	国家自然科学基金重点项目
19	田 丰	解析玉米“上紧下松”耐密株型建成的遗传基础	32330077	国家自然科学基金重点项目
20	李大伟	Metacaspase 家族蛋白在大麦条纹花叶病毒侵染中的功能及分子机制解析	32330086	国家自然科学基金重点项目
21	田长富	近缘快生大豆根瘤菌定殖根际的功能基因网络解析	32430004	国家自然科学基金重点项目



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
22	杨小红	玉米籽粒油分与淀粉含量协同调控的遗传基础	32430075	国家自然科学基金重点项目
23	杨淑华	Ca ²⁺ 信号参与植物低温胁迫应答的分子调控机制研究	31920103002	国家自然科学基金国际（地区）合作与交流项目
24	李召虎	Mn3O4 纳米拟酶提高棉花抗旱性的生理分子机制	32120103008	国家自然科学基金国际（地区）合作与交流项目
25	王 毅	植物感受和适应低钾胁迫的分子机制	32161133014	国家自然科学基金国际（地区）合作与交流项目
26	张永亮	BSR1 免疫受体介导抗大麦条纹花叶病毒的分子机制解析	32320103003	国家自然科学基金国际（地区）合作与交流项目
27	傅 缨	植物适应非生物胁迫过程中细胞骨架介导的生长调控机制研究	2022YFE0108200	国家重点研发计划政府间国际科技创新合作项目
28	陈艳梅	玉米 CPK 激酶抵抗高光胁迫分子机理及其在耐高光种质创新中的应用分析	2023YFE0109500	国家重点研发计划政府间国际科技创新合作项目
29	田长富	根瘤菌多效转录因子 MucR1 寡聚化机制及其对适应性进化的影响	32070078	国家自然科学基金面上项目
30	杨永青	类受体激酶 GSO1 响应盐胁迫的分子机制研究	32070301	国家自然科学基金面上项目
31	王 瑜	转录因子 ZmAL14 在调节玉米干旱胁迫响应中的作用	32070308	国家自然科学基金面上项目
32	李 媛	拟南芥 MPK3/MPK6 介导的细胞壁应答盐胁迫机制研究	32070310	国家自然科学基金面上项目
33	朱 蕾	拟南芥 PUB30 介导的 HB24 泛素化降解途径参与盐胁迫诱导的根生长调控的机制研究	32070311	国家自然科学基金面上项目
34	周文焜	植物 RBR 蛋白网络调控根尖干细胞损伤修复的分子机制	32070874	国家自然科学基金面上项目
35	张明才	赤霉素与 ZmNRT2.1 互作调控玉米根系氮素吸收的机制研究	32071920	国家自然科学基金面上项目
36	李景睿	盐胁迫下 SOS2 通过磷酸化 SE 精准调控表观遗传和基因表达的分子机制	32170283	国家自然科学基金面上项目
37	王良省	叶绿体蛋白 SAFE1 和 SAFE2 介导单线态氧信号转导的机理研究	32170284	国家自然科学基金面上项目
38	苏 震	系统解析水稻脱分化和再分化过程的染色质修饰和转录调控机制	32170673	国家自然科学基金面上项目
39	毛同林	微管结合蛋白 MREL57 参与调控 ABA 诱导保卫细胞运动的生物学机制	32170682	国家自然科学基金面上项目
40	杨光辉	植物根细胞钾离子转运的结构基础	32171188	国家自然科学基金面上项目



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
41	刘升学	玉米 Reticulons 家族蛋白基因 ZmRB16 调控玉米抗旱性的功能研究	32171940	国家自然科学基金面上项目
42	李大伟	大麦条纹花叶病毒 yb 蛋白抑制叶绿体自噬以延缓叶片衰老的分子机制	32270168	国家自然科学基金面上项目
43	任东涛	拟南芥叶绿素合成途径谷氨酸-1-半醛氨基转移酶 GSA1 的磷酸化及磷酸化对 GSA1 功能调控的研究	32270271	国家自然科学基金面上项目
44	周文焜	盐胁迫诱导根尖分生组织细胞死亡的分子机理研究	32270299	国家自然科学基金面上项目
45	徐娟	“长寿基因” LRF1 调控植物叶片衰老的分子机制研究	32270348	国家自然科学基金面上项目
46	杨志蕊	ZmDT10 基因调控干旱胁迫下玉米雌雄穗发育协调性的分子机制	32272024	国家自然科学基金面上项目
47	施怡婷	ZmHSFn 调控玉米耐冷性的分子机制	32272025	国家自然科学基金面上项目
48	段留生	ZmmiR164e 介导赤霉素信号通路调控玉米节间伸长的分子机制	32272036	国家自然科学基金面上项目
49	焦健	根瘤菌锌指蛋白 MucR1 介导外源基因沉默的分子机制	32370086	国家自然科学基金面上项目
50	徐凌	玉米抗旱根系微生物组与宿主的互作机制	32370131	国家自然科学基金面上项目
51	王献兵	富含甘氨酸 RNA 结合蛋白促进植物弹状病毒侵染的分子机制	32370154	国家自然科学基金面上项目
52	陈益芳	植物蛋白激酶 PSRK1 响应环境磷水平变化和调控植物磷稳态的分子机制	32370272	国家自然科学基金面上项目
53	陈立群	拟南芥 eiF4A1/2 与 ERdj3A/3B 相互作用调控生殖发育的分子机制	32370367	国家自然科学基金面上项目
54	陈艳梅	蛋白磷酸酶 NRPP1 介导的去磷酸化途径调控低氮应答的分子机制	32370430	国家自然科学基金面上项目
55	毛传澡	水稻 LCRN1 调控根粗的分子机制解析	32372806	国家自然科学基金面上项目
56	杨萌	叶绿体外膜蛋白 Toc75-III 促进大麦条纹花叶病毒侵染的分子机制解析	32470150	国家自然科学基金面上项目
57	梁鹏博	蒺藜苜蓿-根瘤菌共生互作中 MtINFO 调控根瘤菌胞内侵染的分子机制	32470259	国家自然科学基金面上项目
58	丁杨林	类受体激酶复合体 HRK1-HRK2 调控植物响应高温胁迫的分子机制	32470305	国家自然科学基金面上项目
59	王良省	SOF2 感知及介导叶绿体单线态氧信号的机理研究	32470311	国家自然科学基金面上项目
60	李景睿	SOS2-BRM 模块通过表观遗传调控盐胁迫响应基因表达的分子机制	32470315	国家自然科学基金面上项目



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
61	段留生	乙烯响应因子 EREB131 调控玉米营养生长时相转变和花序发育的分子机制	32472031	国家自然科学基金面上项目
62	张明才	硝态氮介导玉米根系建成的赤霉素信号响应与调控机制	32472035	国家自然科学基金面上项目
63	田晓莉	GhZAT10 整合茉莉酸和乙烯途径协同同调控 GhKUP3 介导的棉花高亲和 K⁺ 吸收机制	32472048	国家自然科学基金面上项目
64	段留生	乙烯响应因子 ZmEREB209 和 ZmEREB147 调控玉米籽粒脱水的分子机制	32472228	国家自然科学基金面上项目
65	徐 娟	MAPK 级联信号调控侧根起始的分子机制研究	32200266	国家自然科学基金青年项目
66	郑绍建	类受体激酶 R450 调控铝离子受体 ALR1 活性及其复合体功能的分子机制研究	32400209	国家自然科学基金青年项目
67	杨志蕊	ZmAGO4 调控玉米响应干旱胁迫的分子机制	32101657	国家自然科学基金青年项目
68	李长江	NF-Y 复合体介导 JA-JAZ8 信号途径调控拟南芥响应高盐胁迫的分子机制研究	32200261	国家自然科学基金青年项目
69	王向锋	微管结合蛋白 SPR1 参与调控植物细胞自噬的分子机理	32200285	国家自然科学基金青年项目
70	梁鹏博	蒺藜苜蓿-根瘤菌共生互作中 MtGSL1 调控宿主细胞壁动态重塑的分子机制	32300216	国家自然科学基金青年项目
71	刘建祥	拟南芥 E3 泛素连接酶 MIEL1 协调环境温度与胚轴伸长的分子机制	32400225	国家自然科学基金青年项目
72	郑绍建	类受体胞质激酶 SRH 调控拟南芥根毛伸长的分子机制	32400274	国家自然科学基金青年项目
73	徐 凌	苏打盐碱地根际微生物提高饲料作物苜蓿、玉米盐碱抗性的作用机制	U23A20151	国家自然科学基金区域创新发展联合基金项目
74	李继刚	密植弱光胁迫下玉米向光生长和叶绿体聚光运动的分子机制研究	U23A20177	国家自然科学基金区域创新发展联合基金重点项目
75	徐明良	玉米广谱抗穗粒腐病基因的克隆及遗传机制解析	U2004205	国家自然科学基金地区联合重点项目
76	田长富	广谱结瘤基因回路的人工设计与系统优化	2019YFA0904704	国家重点研发计划
77	杨淑华	蛋白复合物调控温度信号转导的机理研究	2020YFA0509902	国家重点研发计划
78	毛传澡	水稻小麦磷钾高效利用性状形成的分子调控网络	2021YFF1000402	国家重点研发计划
79	刘建祥	适应土壤环境的水稻小麦养分高效和高产潜力协同机制	2021YFF1000404	国家重点研发计划



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
80	王 毅	玉米磷、钾高效利用性状形成的分子调控网络	2021YFF1000502	国家重点研发计划
81	杨淑华	粮食作物响应低高温与低光胁迫的遗传与分子调控网络	2022YFF1001603	国家重点研发计划
82	田长富	高效利用碳源和能量的固氮菌底盘设计及优化适配	2022YFA0912101	国家重点研发计划
83	郭 岩	植物离子信号感受与应答的大分子研究	2022YFA1303400	国家重点研发计划
84	郑绍建	酸铝离子感受和应答关键蛋白质的功能与结构解析	2022YFA1303402	国家重点研发计划
85	田 丰	复杂性状全基因组选择新方法开发	2022YFD1201503	国家重点研发计划
86	杨小红	玉米抗病虫高产基因资源挖掘与利用-玉米产量相关性状的关键基因挖掘和鉴定	2022YFD1201804	国家重点研发计划
87	杨永青	玉米 SOS 途径调控盐胁迫下 Na ⁺ 稳态及可塑性生长的分子机制	2022YFF1001601-2	国家重点研发计划
88	巩志忠	粮食作物响应水分胁迫的遗传与分子调控网络	2022YFF1001602	国家重点研发计划
89	杨淑华	主粮作物耐盐碱等环境胁迫的遗传机制（课题 3：粮食作物响应低高温与低光胁迫的遗传与分子调控网络）	2022YFF1001603	国家重点研发计划
90	刘建祥	粮食作物响应低高温与低光胁迫的遗传与分子调控网络	2022YFF1001603	国家重点研发计划
91	任东涛	玉米抗逆关键基因位点挖掘与应用	2023YFD1200502	国家重点研发计划
92	于静娟	特色经济作物耐逆调控基因挖掘与利用	2023YFD1200702	国家重点研发计划
93	陈其军	精准基因敲入技术与农作物种质创制	2023YFD1202905	国家重点研发计划
94	段留生	作物提质增效绿色调节剂研制与应用示范	2023YFD1700605	国家重点研发计划
95	周文焜	粮食作物生长发育与环境响应的平衡调控机制研究（子课题）	2023YFF1001300	国家重点研发计划
96	秦 峰	主粮作物生长发育与干旱胁迫耐受平衡调控机制解析	2023YFF1001302	国家重点研发计划
97	周文焜	作物基于相分离感受盐胁迫的机理研究	2023YFF1002100	国家重点研发计划 青年科学家项目
98	段留生	玉米高产宜机收优异基因资源挖掘与利用	2023YFD1201800	国家重点研发计划 青年科学家项目
99	段留生	中低产田玉米协同抵御干旱冷害复合胁迫的调控机制与靶向产品研发	2023YFD1901700	国家重点研发计划 青年科学家项目
100	杨志蕊	玉米抗逆种质资源精准鉴定与优异等位基因挖掘	2021YFD1200703-5	国家重点研发计划 子课题
101	段留生	作物水效率多要素协同提升技术与装置	202310210910085	国家重点研发计划 子课题
102	寿惠霞	大豆产量和品质协同调控分子网络	2021YFF1001204	国家重点研发计划 子课题



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
103	毕国志	甜高粱抗病分子机制研究及单宁和纤维相关基因挖掘	2023YFF1001402	国家重点研发计划子课题
104	王良省	自主知识产权玉米基因编辑体系建立和新种质创制	2023YFF1000203-2	国家重点研发计划子课题
105	王成龙	玉米重要性状形成的结构变异鉴定	2023YFF1000401-2	国家重点研发计划子课题
106	毛传澡	磷钾高效利用新基因挖掘与育种价值	2023ZD040720203	科技创新 2030 项目子课题
107	王喜庆	智能设计育种技术创新与应用	2023ZD0407602	科技创新 2030 项目子课题
108	张永亮	植物抗病毒免疫国际合作与交流	G2023108007L	科技部高端外国专家引进项目
109	丁杨林	非 XXXX 升	非 XXXX 升-2023	国家重大专项子课题
110	施怡婷	耐非生物逆境新基因挖掘与育种价值评价	2023ZD04071	农业生物育种国家科技重大专项
111	王喜庆	玉米高通量自动化表型鉴定装备研发	2022ZD0401801	农业生物育种国家科技重大专项子课题
112	田晓莉	高产广适棉花良种良法配套和规模化示范应用	2023ZD04039-05	农业生物育种国家科技重大专项子课题
113	杨志蕊	玉米抗旱新基因挖掘与育种价值评价	2023ZD040710101	农业生物育种国家科技重大专项子课题
114	程金魁	抗旱耐涝新基因挖掘与育种价值评价	2023ZD040710102	农业生物育种国家科技重大专项子课题
115	张 静	玉米氮高效基因和材料的挖掘与利用	2023ZD040720106	农业生物育种国家科技重大专项子课题
116	陈益芳	优化作物体内磷钾分配利用新基因挖掘与育种价值评价	2023ZD040720204	农业生物育种国家科技重大专项子课题
117	徐明良	东 XXX 用-2024	NK202307020101	农业生物育种国家科技重大专项子课题
118	徐明良	东 XXX 用-2023	NK202307020101	农业生物育种国家科技重大专项子课题
119	张永亮	NYGG	NK202201030102	NYGG 项目
120	刘升学	耐 XXX 估	NK202307030109	NYGG 项目
121	杨小红	NYGG	NK2023070403	NYGG 项目
122	杨光辉	农 XX 术-2023	NK20231701	NYGG 项目
123	田晓莉	现代农业产业技术体系-棉花-化学调控	CARS-15-16	现代农业产业技术体系项目



序号	姓名	项目（课题）名称	项目（课题）编号	项目类别
124	李继刚	TZP 蛋白 SUMO 化修饰调控植物远红光信号转导的分子机理	5232011	北京市自然科学基金面上项目
125	陈立群	玉米转录因子 GRAS32 调控根毛生长和铁胁迫响应的分子机制	6232016	北京市自然科学基金面上项目
126	田长富	土壤健康与耕地可持续承载能力提升集成技术研发与试验示范	SZJBGS202301	安徽省宿州市接榜挂帅课题
127	郑绍建	华南红壤耕地生态健康修复与提升的关键过程与调控技术研究	NT202010	广东省实验室处方科研项目
128	寿惠霞	油菜等旱粮作物基因资源利用数据库及交互式门户网站的建立	2021C02055	浙江省科技计划项目
129	徐 娟	MAPK 级联调控种子大小的分子机制研究	LZ23C020003	浙江省自然科学基金重点项目
130	毛传澡	水稻根构型的分子调控机制解析	Z24C150004	浙江省自然科学基金重点项目
131	毛传澡	水稻复合逆境的协同响应机制及其在育种中的利用	LD24C30002	浙江省自然科学基金重大项目子课题
132	徐 娟	多个根发育过程中 MPK3/MPK6 底物的系统鉴定	Y23C020009	浙江省自然科学基金一般项目



九、国内外学术交流

(一) 邀请国内外同行讲学

序号	邀请人	报告人姓名、单位	报告题目	报告日期
1	汪 洋	高欣, 沙特阿卜杜拉国王科技大学	人工智能赋能植物科学之浅见	2024.02.18
2	杨淑华	李文学, 中国农业科学院作物科学研究所	玉米籽粒富铁基因的挖掘及利用	2024.03.07
3	杨淑华	钱伟强, 北京大学	DNA 甲基化的动态调控和生物学功能	2024.03.14
4	杨淑华	张阳, 四川大学	植物代谢的多层次调控	2024.03.28
5	杨淑华	童红宁, 中国农业科学院作物科学研究所	油菜素甾醇 BR 作用机制解析与利用	2024.03.28
6	杨淑华	杨扬, Cell Press	Getting your paper published at cell press	2024.04.11
7	王良省	Bernhard Grimm, Humboldt University of Berlin (洪堡大学)	Recent advances in research into flavin biosynthesis and heme synthesis	2024.04.12
8	郑绍建	Moussa Benhamed, 巴黎大学	Advances in epigenetics	2024.04.12
9	杨光辉	杨帆, 浙江大学	TRP 通道的配体门控机制与镇痛分子开发	2024.04.13
10	杨淑华	严顺平, 华中农业大学	植物 DNA 损伤应答机理	2024.04.17
11	寿惠霞	刘栋, 清华大学	低磷胁迫调控根构型重塑的分子机制	2024.04.19
12	杨淑华	鲁非, 中国科学院遗传与发育生物学研究所	小麦演化历史的群体遗传学解析	2024.04.25
13	杨淑华	朱旺升, 中国农业大学	小肽门控钙通道在植物先天免疫中的作用	2024.05.09
14	张永亮	Peter Andrew Moffett, Université de herbrooke	Building a niche: How pathogens create favourable environments for growth	2024.05.15
15	毛传澡	侯兴亮, 中国科学院华南植物园	多倍体作物甘薯重要性状遗传机理的研究探索	2024.05.17
16	刘建祥	Seth Davis, 约克大学	Quantitative responses via circadian-clock variation: lab and field studies in <i>Arabidopsis</i>	2024.05.21
17	毛传澡	Laurent Nussaume, 法国艾克斯-马赛大学	Interest of live transcriptional imaging to study phosphate homeostasis	2024.05.22
18	杨淑华	闫建斌, 中国农业科学院农业基因组研究所	抗癌明星药物紫杉醇的生物合成与合成生物学制造	2024.05.30
19	杨淑华	李传友, 山东农业大学, 中国科学院遗传与发育生物学研究所	植物再生因子的发现与应用	2024.05.30



序号	邀请人	报告人姓名、单位	报告题目	报告日期
20	王喜庆	董楠卿, 上海人工智能实验室	AI for science: 人工智能驱动的科学研究的科学研究	2024.06.20
21	张永亮	谷杨楠, University of California, Berkeley	Proximity labeling-driven understanding of the plant nuclear envelope	2024.07.24
22	杨淑华	Dae-Jin Yun, Konkuk University (建国大学)	Cold stress induced dynamic chromatin accessibility in <i>Arabidopsis</i>	2024.08.06
23	杨淑华	Woe-Yeon Kim, Gyeongsang National University (庆尚大学)	Diurnal regulation of root growth by circadian clock in <i>Arabidopsis</i>	2024.08.06
24	杨淑华	Isabel Bäurle, University of Potsdam (波茨坦大学)	How plants remember a stressful day – a role for chromatin-based mechanisms	2024.08.06
25	杨淑华	Kyuha Choi, Pohang University of Science and Technology (浦项科技大学)	Control of meiotic crossover patterning in <i>Arabidopsis</i>	2024.08.06
26	杨淑华	Michael Lenhard, University of Potsdam (波茨坦大学)	Telling left from right - the genetic and molecular basis of enantiostry in wachendorfia and barberetta	2024.08.06
27	杨淑华	Young Hun Song, Seoul National University (首尔国立大学)	Effect of red to far-red light on development and stress responses in <i>Arabidopsis</i>	2024.08.07
28	梁鹏博	Jeremy Murray, John Innes Centre (约翰·英纳斯中心)	Sending the right signals: Flavonoid specificity in the legume-rhizobia symbiosis	2024.08.07
29	梁鹏博	Takuya Suzuki, University of Tsukuba (筑波大学)	How plants obtain nitrogen by supplying iron to symbiotic bacteria	2024.08.07
30	王良省	Dario Leister, The University of Munich (慕尼黑大学)	Photosynthetic cyclic electron flow	2024.08.07
31	秦 峰	郭惠珊, 中国科学院微生物所	棉花-轮枝菌互作和抗病 RNAi 研究	2024.09.20
32	杨光辉	闫湔, 西湖大学	叶绿体蛋白转运机制研究	2024.09.25
33	周文焜	吴双, 福建农林大学	番茄表皮改造与绿色生产	2024.09.27
34	毛传澡	孙博, 南京大学	Capture of regulatory factors via CRISPR-dCas9 for mechanistic analysis of fine-tuned <i>SERRATE</i> expression in <i>Arabidopsis</i>	2024.09.28
35	毛传澡	Toshiro Ito, 奈良先端科学技术大学院大学	Deciphering plant reproduction: The role of agamous in hermaphroditic strategies	2024.09.28
36	梁鹏博	杨青, 中国农业科学院植物保护研究所	植物病虫害的几丁质相关生物学机制	2024.10.11
37	郑绍建	吴双, 福建农林大学	番茄表皮改造与绿色生产	2024.10.11



序号	邀请人	报告人姓名、单位	报告题目	报告日期
38	郑绍建	王存, 西北农林科技大学	植物营养中的钙信号—以锰元素为例	2024.10.11
39	郑绍建	丁兆军, 山东大学	生长素是调控植物根系可塑性生长发育的重要调控因子	2024.10.11
40	秦 峰	戚益军, 清华大学	植物中的 RNA 调控	2024.10.18
41	寿惠霞	杨万能, 华中农业大学	作物表型组学技术进展与育种应用	2024.10.23
42	傅 纓	Shaul Yalovsky, Tel Aviv University (特拉维夫大学)	Molecular switches: mastering stomatal control	2024.11.05
43	傅 纓	巫永睿, 中国科学院分子植物科学卓越创新中心	Molecular genetic basis of dent kernel improvement in maize	2024.11.05
44	傅 纓	徐通达, 福建农林大学	Perception and signal transduction mechanisms of extracellular auxin in plants	2024.11.05
45	傅 纓	Roy Weinstain, Tel Aviv University (特拉维夫大学)	Slow release of a synthetic auxin induces formation of adventitious roots in recalcitrant woody plants	2024.11.05
46	傅 纓	丁兆军, 山东大学	Auxin facilitates lateral root salt avoidance via activating SOS1	2024.11.05
47	傅 纓	Nir Sade, Tel Aviv University (特拉维夫大学)	Elucidating the physiological and molecular function of candidate genes regulating root hydraulic architecture of monocots and dicots	2024.11.05
48	傅 纓	熊立仲, 华中农业大学	Phenomics accelerates drought resistance gene discovery and application	2024.11.05
49	傅 纓	张立新, 河南大学	Structural and functional dynamics of photosynthetic protein complexes during light acclimation	2024.11.05
50	傅 纓	刘宏涛, 深圳大学	The blue-light receptor CRY1 serves as a switch to balance photosynthesis and defense	2024.11.05
51	傅 纓	Hilla Keidan Toporik, The Hebrew University of Jerusalem (耶路撒冷希伯来大学)	Modularity and heterogeneity in photosynthetic antenna systems	2024.11.05
52	傅 纓	周文彬, 农业科学院作物科学研究所	Physiological and molecular responses to high light stress in maize and rice	2024.11.05
53	傅 纓	Yotam Zait, The Hebrew University of Jerusalem (耶路撒冷希伯来大学)	Reengineer crops for a changing climate	2024.11.06
54	傅 纓	Tzachi Arazi, Volcani Institute (以色列农业研究中心)	MADS gatekeepers: ovule protein complexes ensure fertilization-dependent fruit set	2024.11.06



序号	邀请人	报告人姓名、单位	报告题目	报告日期
55	傅 缨	王永红, 山东农业大学	A novel cytokinin transporter contributes to panicle development and nitrogen use efficiency in rice	2024.11.06
56	傅 缨	钱伟强, 北京大学	Alba proteins confer thermotolerance at seedling and reproductive stages through stabilizing specific mRNAs in stress granules	2024.11.06
57	傅 缨	郭晓玉, 中国科学院植物所	Temperature sensing and genetic basis for chilling tolerance in rice	2024.11.06
58	傅 缨	Lidor Shaar Moshe, Haifa University (海法大学)	Unraveling the cellular basis of salt tolerance in tomato	2024.11.06
57	傅 缨	Tamar Avin Wittenberg, The Hebrew University of Jerusalem (耶路撒冷希伯来大学)	Exploring stress-related sugars as plant autophagy regulators	2024.11.06
60	傅 缨	Rachel Amir, Tel Hai College (德海学院)	Cysteine redistribution during oxidative stress: balancing glutathione and methionine for plant protection at the cost of growth	2024.11.06
61	傅 缨	Robert Fluhr, Weizmann Institute (韦兹曼科学研究所)	Stress-generated singlet oxygen: a short-life molecule with everlasting effects	2024.11.06
62	傅 缨	宫磊, 东北师范大学	Organellar genome divergence and stress response shape the cytonuclear co-evolution coordination within alloplasmic cybrids	2024.11.06
63	傅 缨	Simon Barak, Ben Gurion University (本·古里安大学)	Stress-ready or stress-reactive? That is the extremophyte question	2024.11.06
64	傅 缨	王晓杰, 西北农林科技大学	Infection strategy of biotrophic rust fungi: invasion and manipulation of host immune responses	2024.11.06
65	傅 缨	高彩霞, 中国科学院遗传与发育研究所	Precision genome editing for future agriculture	2024.11.06
66	杨淑华	郭红卫, 南方科技大学	DCP5 介导的植物渗透感应新机制	2024.11.08
67	田长富	徐健, 中国科学院青岛生物能源与过程所	农业单细胞原位代谢图谱计划: 从元拉曼组平台开始	2024.11.15
68	杨淑华	黄飞, 北京大学	Epigenetic control of gene expression by cellular metabolisms in plants	2024.11.15
69	郑绍建	孔凡江, 广州大学	大豆光周期开花与株型调控	2024.12.08



序号	邀请人	报告人姓名、单位	报告题目	报告日期
70	郑绍建	杨文强，中国科学院植物研究所	叶绿体蛋白转运与质量控制	2024.12.08
71	郑绍建	李继刚，中国农业大学	远红光信号转导的分子机制	2024.12.08
72	郑绍建	钦鹏，四川农业大学	水稻耐热遗传基础解析及应用	2024.12.08



(二) 在国内外参加会议报告

序号	报告人	报告题目	会议名称	会议日期
1	梁鹏博	An evolutionarily shared formin protein INFO-mediated different symbiotic intracellular infections in legume and non-legume plants	第 6 届亚太植物-微生物共生固氮大会	2024.01.07
2	田长富	Optimization mechanisms for symbiotic function of broad-host-range Sinorhizobium fredii	第 6 届亚太植物-微生物共生固氮大会	2024.01.07
3	焦 健	Deciphering the pH adaptation of faba bean rhizobia via comparative genomics	第 6 届亚太植物-微生物共生固氮大会	2024.01.07
4	徐明良	玉米抗灰斑病的遗传基础，分子机制和育种应用	2024 年 New Crops 玉米生物学高峰论坛	2024.01.13
5	王喜庆	现代玉米育种大田表型技术现状与发展趋势	第十届全国玉米育种大会	2024.03.02
6	杨小红	玉米高产优质的协调与改良	第十届植物生物学女科学家学术交流会	2024.03.20
7	杨小红	玉米籽粒油分合成和积累的遗传基础	中国农业大学-扬州大学 2024 年作物学高峰论坛	2024.04.23
8	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 的创制、功能研究与应用	第八届生物刺激剂与农业绿色发展大会	2024.04.17
9	陈丽梅	创新平台提供一流服务	第七届全国玉米生物学学术研讨会	2024.04.25
10	徐明良	玉米 WAK/WAKL 激酶的抗病机制研究	第七届全国玉米生物学学术研讨会	2024.04.25
11	张永亮	植物抗病毒免疫新功能模块鉴定和分子机制解析	2024 年整合植物生物学前沿学术研讨会暨 JIPB 编委会	2024.05.10
12	张 静	植物根系可塑性生长机制研究	2024 年整合植物生物学前沿学术研讨会暨 JIPB 编委会	2024.05.10
13	丁杨林	植物应答温度胁迫早期信号的分子机制	2024 年整合植物生物学前沿学术研讨会暨 JIPB 编委会	2024.05.10
14	王 毅	第一届植物养分调控与高效利用国际研讨会	第一届植物养分调控与高效利用国际研讨会	2024.05.11
15	毛传澡	Molecular regulatory mechanisms of phosphate uptake and signaling in rice	第一届植物养分调控与高效利用国际研讨会	2024.05.11
16	寿惠霞	Phosphate-dependent regulation of vacuolar trafficking of OsSPX-MFSs is critical for maintaining intracellular phosphate homeostasis in rice	第一届植物养分调控与高效利用国际研讨会	2024.05.11



序号	报告人	报告题目	会议名称	会议日期
17	梁鹏博	Evolutionarily conserved formin protein facilitates intracellular symbiotic microbe infections in legume and non-legume plants	植物微生物互作多学科交叉国际研讨会	2024.05.15
18	徐明良	ZmWAKL 介导的玉米灰斑病抗性机制	第二届小麦生物育种高峰论坛	2024.05.18
19	毛传澡	水稻养分高效根构型的分子机制及遗传改良	2024 峡山会议	2024.05.24
20	郑绍建	植物细胞铝离子受体及其信号转导通路	2024 峡山会议	2024.05.25
21	王 毅	植物氮钾高效分配利用的调控机制	2024 峡山会议	2024.05.26
22	王喜庆	选好地、种好地：气象与育种、栽培的结合	中国气象局公共气象服务中心学术交流周“大语言模型+行业”专场报告会	2024.05.30
23	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 和威普绿 (VIP) 的创制与应用	齐鲁基因组生物学学术论坛	2024.06.24
24	杨淑华	Molecular regulation of cold tolerance in <i>Arabidopsis</i> and maize	13 th International Congress of Plant Molecular Biology	2024.06.24
25	梁鹏博	Beyond Legumes: Harnessing symbiotic insights for revolutionary nitrogen fixation in non-legume crops	aBIOTECH Conference-代谢工程助力农业科技创新	2024.06.27
26	杨小红	玉米籽粒类胡萝卜素基因挖掘及其育种应用初探	东方科技论坛-新质生产力赋能玉米重大品种创制研讨会	2024.06.30
27	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 和威普绿 (VIP) 的创制与应用	第一届全国作物杂种优势与生物育种学术大会	2024.07.01
28	蒋才富	玉米耐盐碱的分子机理及生物育种	第一届全国作物杂种优势与生物育种学术大会	2024.07.01
29	杨小红	玉米籽粒类胡萝卜素基因挖掘及其育种初探	2024 中国 (武清) 北方鲜食玉米大会	2024.07.05
30	杨淑华	Molecular mechanisms of plant response to cold stress	The 11 th International Horticulture Research Conference	2024.07.14
31	梁鹏博	Evolutionarily conserved formin proteins facilitate intracellular symbiotic microbe infections in legume and non-legume plants	全国生物固氮大会	2024.07.18
32	焦 健	蚕豆根瘤菌土壤 pH 适应的遗传机制的比较基因组学解析	全国生物固氮大会	2024.07.18
33	丁杨林	植物低温特异钙信号的产生与解码机制	2024 生物物理大会	2024.07.26
34	郑绍建	植物铝离子受体及其信号转导	第三届中国植物修复生物学学术研讨会	2024.07.26
35	郭 岩	植物耐盐机理研究	2024 年植物逆境适应机制国际学术研讨会	2024.08.01



序号	报告人	报告题目	会议名称	会议日期
36	王献兵	Plant rhabdovirus regulates activity of insect vectors for efficient transmission	Asian Conference on Plant Pathology 2024	2024.08.03
37	李长江	植物响应不同程度盐胁迫的分子机制	第九届全国植物生物学与植物逆境生物学研讨会	2024.08.03
38	丁杨林	Mechanism of heat stress responses regulated by receptor-like kinases in plants	植物逆境应答与环境适应性学术研讨会	2024.08.06
39	宋 文	Biochemical mechanism of TIR-triggered plant immunity	植物逆境应答与环境适应性学术研讨会	2024.08.06
40	李继刚	Phosphorylation mechanism of the phyA photoreceptor	植物逆境应答与环境适应性学术研讨会	2024.08.06
41	杨光辉	土地盐碱化下的植物钠钾离子稳态调节	全国农业生物化学与分子生物学第二十一次学术研讨会	2024.08.09
42	郑绍建	植物抗铝研究-暨植物铝离子受体的发现及其信号转导通路解析	2024 中国植物营养与肥料学会学术年会	2024.08.09
43	陈丽梅	矮化抗倒易机收玉米种质创新与利用	第一届玉米种质改良与创新利用研讨会	2024.08.10
44	杨小红	玉米产量性状遗传解析与基因发掘	第一届玉米种质改良与创新利用研讨会	2024.08.10
45	田 丰	玉米耐密株型建成的分子遗传基础	第十二届全国小麦基因组与分子育种大会	2024.08.16
46	田 丰	Maize smart-canopy architecture enhances yield at high densities	第二十三届全国植物基因组大会	2024.08.19
47	徐明良	A calcium-dependent protein kinase mediates quantitative resistance to multiple foliar diseases in maize	第二十三届全国植物基因组大会	2024.08.22
48	周文焜	Root dynamic growth in response to stress: A stem cell perspective	中国植物生理与植物分子生物学学会 2024 年全国学术年会暨第十三次全国会员代表大会	2024.08.25
49	施怡婷	玉米耐冷性的遗传与分子机制	中国植物生理与植物分子生物学学会 2024 年全国学术年会暨第十三次全国会员代表大会	2024.08.25
50	张 静	硝酸盐调控植物根系可塑性生长的分子机制研究	中国植物生理与植物分子生物学学会 2024 年全国学术年会暨第十三次全国会员代表大会	2024.08.25



序号	报告人	报告题目	会议名称	会议日期
51	郑绍建	植物铝离子受体及其信号转导	中国植物生理与植物分子生物学学会 2024 年全国学术年会暨第十三次全国会员代表大会	2024.08.27
52	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 的创制、功能研究与应用	第二届植物免疫诱抗剂暨生物刺激剂发展交流会	2024.09.05
53	徐明良	玉米重要抗病基因克隆和分子育种	2024 年全国玉米遗传育种研讨会	2024.09.05
54	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 和威普绿 (VIP) 的创制与应用	河南省作物绿色生产科技论坛	2024.09.06
55	田 丰	玉米耐密株型建成的分子遗传基础	中国作物学会第十二次全国会员代表大会暨第二十一届中国作物学会学术年会	2024.09.12
56	杨淑华	植物感知与应答低温胁迫的分子调控机制	Molecular Plant 作物安全与高效生产前沿论坛	2024.09.25
57	巩志忠	主要农作物品种全面提升技术：植物免疫启动蛋白维大力 (VDAL) 和威普绿 (VIP) 的创制与应用	2024 世界农业科技创新大会 (WAFI) 中阿-中亚-南亚旱地农业边会	2024.10.11
58	李继刚	Molecular mechanism of far-red light signaling	植物合成生物学前沿论坛	2024.10.11
59	王献兵	Plant virus-encoded viroporins: biological functions and inhibitor screening	The 7 th International Conference on Biotic Plant Interactions	2024.10.13
60	田长富	Symbiotic compatibility mediated by nonorthogonal integration of key symbiosis genes in broad-host-range rhizobia	植物-生物互作国际会议	2024.10.14
61	王喜庆	万物皆数，种地可以吗？	数理化基础学科涉农交叉创新论坛	2024.10.15
62	杨光辉	土地盐碱化下的植物钠钾离子稳态调节	2024 年全国电子显微学学术年会	2024.10.17
63	王喜庆	良种佳缘--品种定位、销售、交易数据化支撑系统	第三十一届中国北京种业大会--第四届中国玉米种子及产业链专业论坛	2024.10.18
64	李继刚	远红光信号转导的分子机制	第四届全国植物光生物学大会	2024.10.18
65	张永亮	植物病毒复制复合体的三维结构与组分解析	2024 年全国电子显微学学术年会	2024.10.18
66	田长富	耐盐碱大豆根瘤菌的逆境适应与共生固氮协同调控机制	障碍土壤的微生物修复技术学术研讨会	2024.10.18



序号	报告人	报告题目	会议名称	会议日期
67	巩志忠	The technology for updating Crop variety: The application of VDAL and VIP protein	World life Science Conference WLSC2024	2024.10.19
68	杨淑华	Stomata regulation of cold tolerance in plants	46 th New Phytologist Symposium	2024.10.21
69	李继刚	Melecular mechanism of phytochrome A signaling	2024 光合作用国际研讨会	2024.10.24
70	杨 萌	大麦条纹花叶病毒与叶绿体的相互作用	中国植物病理学会病毒专业委员会和植物与病原物互作专业委员会 2024 年学术年会	2024.10.25
71	王献兵	小肽自噬受体 VISP1 在病毒侵染中作用机制	中国植物病理学会病毒专业委员会和植物与病原物互作专业委员会 2024 年学术年会	2024.10.25
72	杨永青	“良种佳缘”模型助力我国玉米稳产高产	第二届农业农村大数据大会暨第十届农业模型开发和应用大会	2024.10.26
73	巩志忠	ABA 信号传递和气孔运动	第十一届全国功能基因组学高峰论坛	2024.10.26
74	郑绍建	植物细胞铝离子受体及其信号转导通路	林木生物技术学科群学术研讨会	2024.10.31
75	杨永青	植物应答盐碱胁迫机制解析	全国植物生长发育与环境互作适应研讨会	2024.11.01
76	田 丰	玉米智慧株型建成的分子遗传基础	中国遗传学会 2024 全国学术研讨会	2024.11.03
77	巩志忠	Efficiency and yield increase technologies for major crops: the application of plant immune eliciting proteins VDAL and VIP	The 8 th Yellow River International Forum	2024.11.08
78	李继刚	远红光信号转导的分子机制	2024 年逆境生物学与粮食安全博士后论坛	2024.11.13
79	傅 纓	拟南芥 ECAP-LUG-BEH3 模块调控小孢子母细胞发生	2024 全国植物生物学大会	2024.11.17
80	丁杨林	细胞膜上的受体复合体调控植物早期高温信号的感知与应答机制	2024 全国植物生物学大会	2024.11.17
81	王献兵	钾离子调控植物弹状病毒侵染的分子机理	2024 全国植物生物学大会	2024.11.17
82	张 静	硝酸盐调控植物根系可塑性生长的分子机制研究	2024 全国植物生物学大会	2024.11.17
83	宋 文	植物 TIR 类抗病蛋白激活免疫的生化机制	2024 全国植物生物学大会	2024.11.17
84	陈其军	PE6c 大幅提高了 15 个重要农艺性状基因的引导编辑效率	2024 全国植物生物学大会	2024.11.17
85	杨光辉	盐碱胁迫下植物钠离子转运蛋白活性调节的结构基础	2024 全国植物生物学大会	2024.11.17



序号	报告人	报告题目	会议名称	会议日期
86	寿惠霞	Role of vacuolar phosphate transporters OsSPX-MFSs on maintaining intracellular phosphate homeostasis and their regulation in rice (<i>Oryza sativa</i> L.)	International Conference on Genetic Basis and Molecular Breeding of Abiotic Stress in Rice	2024.11.17
87	傅 缨	SYP121-mediated Exocytosis Participates in stomatal opening in <i>Arabidopsis</i>	2024 Plant Cell Biology	2024.11.29
88	杨永青	植物耐盐碱关键基因挖掘、机制解析及育种利用	2024 全国旱作农业发展与产能协同提升研讨会	2024.12.06
89	郑绍建	植物离子感知与响应的分子机制	生物技术与现代农业创新论坛	2024.12.06
90	田长富	从土壤到根瘤：抗逆广谱高效根瘤菌的选育	多介质协同的土壤科学交叉发展高端论坛	2024.12.07



(三) 在国内外讲学

序号	讲学人	报告题目	讲学单位	讲学日期
1	李继刚	光调控植物逆境响应的分子机制	东北农业大学	2024.01.14
2	梁鹏博	Evolutionarily conserved formin protein facilitates intracellular symbiotic microbe infections in legume and non-legume plant species	日本佐贺大学	2024.03.05
3	田长富	Integration of key symbiosis genes in rhizobia	日本佐贺大学	2024.03.05
4	王喜庆	种植业的新质生产力	深圳市农业科技促进中心	2024.03.11
5	杨淑华	植物激素和光信号调控植物耐低温的分子机制	广州大学	2024.03.19
6	杨淑华	植物抗寒的分子和遗传基础	海南大学	2024.03.23
7	杨淑华	植物耐低温机制研究与种质创新	先正达公司	2024.03.25
8	李继刚	Molecular mechanism of far-red light signaling	四川农业大学	2024.04.01
9	李继刚	远红光信号转导的分子机制	四川大学	2024.04.02
10	宋 文	植物抗病蛋白激活免疫的分子机制	首都师范大学	2024.04.11
11	李继刚	光敏色素 A 信号转导	湖南大学	2024.04.12
12	傅 纓	The regulation of SNARE-mediated membrane fusion in plants	南开大学	2024.04.18
13	田长富	大豆根瘤菌结瘤固氮效率的调控与演化机制	安徽农业大学	2024.04.25
14	丁杨林	类受体激酶调控植物应答高温胁迫的分子机制	山东师范大学	2024.04.28
15	丁杨林	植物感知和响应温度胁迫的分子机制	山东农业大学	2024.04.29
16	李继刚	光敏色素 A 磷酸化的分子机制	湘湖实验室	2024.05.10
17	杨淑华	植物感知与应答低温胁迫的分子与遗传基础	中国科技大学	2024.05.18
18	徐明良	ZmWAKL 介导的玉米灰斑病抗性机制	兰州大学	2024.05.21
19	傅 纓	Regulate SNAREs in plant cells	福建农林大学	2024.05.24
20	杨淑华	植物感知与应答低温信号	中国科学院上海分子植物卓越中心	2024.05.28
21	王喜庆	选好地、种好地--模型与种植的结合	东北农业大学	2024.05.29
22	杨淑华	植物响应低温胁迫的分子机制	山东农业大学	2024.05.31
23	杨淑华	植物感知与应答低温信号的研究进展	清华大学	2024.06.05
24	李继刚	远红光信号转导的分子机制	南开大学	2024.06.06
25	杨淑华	植物耐低温的分子调控机制	南开大学	2024.06.07
26	郭 岩	植物 SOS2 激酶介导的耐盐机制研究	北京大学	2024.06.11
27	杨淑华	植物如何感知与应答低温信号	北京林业大学	2024.06.13
28	郭 岩	植物 SOS2 激酶介导的耐盐机制研究	内蒙古大学	2024.06.25
29	郑绍建	植物细胞铝离子感知及其信号转导	浙江师范大学	2024.06.27
30	毛传澡	作物磷吸收转运、信号及遗传改良	西北农林科技大学	2024.06.28
31	杨淑华	Molecular mechanism of plant responses to cold stress	新加坡国立大学	2024.07.01



序号	讲学人	报告题目	讲学单位	讲学日期
32	郑绍建	植物细胞铝离子受体鉴定及其信号转导通路解析	四川大学	2024.07.11
33	杨淑华	植物如何抵抗寒冷	云南师范大学	2024.07.14
34	李继刚	Molecular mechanism of far-red light signaling	深圳大学	2024.07.22
35	李继刚	Phosphorylation mechanism of the phyA photoreceptor	中山大学农学院	2024.07.23
36	杨淑华	Molecular and genetic basis of cold tolerance in maize	四川大学	2024.08.08
37	杨永青	盐碱胁迫下植物维持细胞离子和 pH 稳态的分子机制	山东师范大学	2024.08.09
38	丁杨林	Mechanism of heat stress responses regulated by receptor-like kinases in plants	西北农林科技大学	2024.08.16
39	郭 岩	科学研究方向的规划设计及建议	宁夏农业科学研究院	2024.09.02
40	徐明良	玉米抗灰斑病基因挖掘与机制研究	山东农业大学	2024.09.04
41	王 毅	NPF-mediated potassium and nitrogen transport in plants	南京农业大学	2024.09.04
42	郭 岩	植物耐盐机理研究	南开大学	2024.09.19
43	徐明良	玉米抗灰斑病研究进展	吉林省农科院	2024.09.20
44	徐明良	玉米抗灰斑病基因及抗性机制	吉林大学	2024.09.21
45	傅 纓	调控植物细胞极性的 ROP GTPases 信号网络	首都师范大学	2024.09.23
46	王良省	叶绿体活性氧产生、感知及耐受的分子机理	华南农业大学	2024.09.25
47	杨淑华	玉米耐低温的分子调控	华中农业大学	2024.10.01
48	徐 娟	MAPK 级联信号调控植物生长发育	山西师范大学	2024.10.09
49	王 毅	NPF-mediated potassium and nitrogen allocation in plants	华南农业大学	2024.10.10
50	郭 岩	植物耐盐机理研究	山东师范大学	2024.10.11
51	李继刚	在酵母中重建受光调控的 ABA 信号通路	华中农业大学	2024.10.17
52	傅 纓	调控植物细胞中的囊泡运输	山西师范大学	2024.10.21
53	寿惠霞	综合多组学方法挖掘作物新基因、功能和机制	山东农业大学	2024.10.24
54	周文焜	Root dynamic growth in response to stress: A stem cell perspective	深圳理工大学	2024.10.30
55	周文焜	Root dynamic growth in response to stress: A stem cell perspective	华南农业大学	2024.10.31
56	张永亮	植物病毒与宿主互作和抗病毒育种	中国科学院大学	2024.11.07
57	李大伟	大麦条纹花叶病毒 yb 蛋白在病毒侵染和致病中的新功能	河南农科院	2024.11.08
58	梁鹏博	Evolutionarily conserved formin proteins facilitate intracellular symbiotic microbe infections in legume and non-legume plants	河南大学	2024.11.14
59	徐明良	植物数量性状基因克隆	山东农业大学	2024.11.18
60	蒋才富	植物耐盐碱研究进展及生物育种	华南农业大学	2024.11.22
61	徐明良	玉米重要抗病基因克隆和利用	江苏省农科院	2024.11.22
62	徐明良	玉米抗灰斑病基因及抗性机制	南京农业大学	2024.11.23



序号	讲学人	报告题目	讲学单位	讲学日期
63	杨永青	“良种佳缘”模型助力玉米育种和品种的稳产高产	塔里木大学	2024.11.25
64	宋 文	植物抗病蛋白激活免疫的分子机制	北京大学	2024.11.29
65	郭 岩	植物盐碱胁迫应答反应 耐盐高效助力国家粮食安全	北京大学	2024.12.04
66	田长富	根瘤菌泛基因组的维持机制	广东省农科院	2024.12.09
67	田长富	模式根际微生物“根瘤菌”兼性共生生活史的演化机制	华南农业大学	2024.12.09



十、学术组织任职

序号	人员姓名	学术组织名称	职务
1	杨淑华	中国植物学会女植物学家分会	会长
2	杨淑华	中国植物生理与植物分子生物学学会	理事
3	杨淑华	中国植物学会	副秘书长 常务理事
4	杨淑华	中国植物生理与植物分子生物学学会植物与环境专业委员会	主任
5	杨淑华	九三学社第十五届中央委员会农林专门委员会	副主任兼秘书长
6	杨淑华	首都女教授协会第六届理事会	常务理事
7	杨淑华	首都女教授协会中国农业大学分会第五届理事会	会长
8	王 毅	中国生物物理学会膜生物学会分会	委员
9	王 毅	中国植物学会细胞生物学专业委员会	委员
10	王 毅	中国遗传学会青年委员会	委员
11	王 毅	中国植物生理与植物分子生物学学会植物与环境专业委员会	委员
12	傅 缨	中国植物学会女植物学家分会	委员
13	傅 缨	中国植物学会植物细胞生物学专业委员会	委员
14	傅 缨	中国植物学会植物结构与生殖生物学专业委员会	委员
15	傅 缨	中国植物生理与植物分子生物学学会植物生物学女科学家分会理事	委员
16	傅 缨	北京细胞生物学会	理事
17	傅 缨	首都女教授协会女科技工作者专委会	委员
18	任东涛	北京生物化学与分子生物学会	常务理事
19	李召虎	中国作物学会	监事长
20	段留生	中国农药应用与发展协会植物生长调节剂专业委员会	主任委员
21	田晓莉	中国作物学会棉花专业委员第一届理事会	委员
22	田晓莉	中国农学会棉花分会第十届理事会	常务理事
23	张明才	中国农学会耕作制度分会第十届委员会	常务理事
24	李继刚	中国细胞生物学学会植物器官发生分会	委员
25	李继刚	中国植物生理与植物分子生物学学会青年工作委员会	委员
26	李继刚	中国植物学会植物生理及分子生物学专业委员会	秘书长
27	田 丰	Maize Genetics Meeting Steering Committee	Asian Representative
28	田 丰	中国作物学会玉米专业委员会	秘书长
29	田 丰	中国作物学会第二届分子育种专业委员会	副秘书长
30	田 丰	中国遗传学会数量遗传学分会	委员
31	杨小红	中国植物学会女植物学家分会	委员
32	王喜庆	中国遗传学会植物表型组分会	委员
33	王喜庆	全国植物新品种测试标准化技术委员会	委员
34	王喜庆	中国生物物理学会表型组学分会	委员
35	陈其军	中国遗传学会基因编辑分会	委员
36	李大伟	中国植物病理学会植物病毒专业委员会	副主委
37	王献兵	中国植物病理学会	理事
38	王献兵	中国植物病理学会植物与病原相互作用专业委员会	副主任委员



序号	人员姓名	学术组织名称	职务
39	王献兵	中国昆虫学会第十一届理事会媒介昆虫与病原互作委员会	委员
40	王献兵	中国微生物学会病毒学专业委员会	委员
41	田长富	农业农村部肥料登记评审委员会	委员
42	田长富	国际根瘤菌与土壤杆菌分类委员会	委员
43	田长富	中国农业生物技术学会	理事
44	田长富	中国农业生物技术学会微生物技术分会	常务理事
45	田长富	中国微生物学会普通微生物学专业委员会	委员
46	田长富	中国微生物学会农业微生物学专业委员会	委员
47	田长富	中国微生物学会微生物资源专业委员会	委员
48	田长富	北京市微生物学会	理事
49	郑绍建	浙江省植物生理与植物分子生物学学会	理事长
50	郑绍建	中国植物生理与植物分子生物学学会	副秘书长
51	刘建祥	浙江省植物生理与植物分子生物学学会	副理事长
52	刘建祥	中国植物生理与植物分子生物学学会	理事
53	寿惠霞	浙江省植物生理与植物分子生物学学会	监事长
54	毛传澡	中国植物营养与肥料学会植物营养分子生理专业委员会	副主任委员
55	毛传澡	浙江省植物生理与植物分子生物学学会	秘书长
56	徐纪明	浙江省植物生理与植物分子生物学学会	副秘书长



十一、学术期刊任职

序号	人员姓名	期刊名称	职务
1	杨淑华	Plant Cell	Reviewing Editor
2	杨淑华	New Phytologist	Editor
3	杨淑华	Science China-Life Science	Editor
4	杨淑华	Journal of Integrative Plant Biology	Editor
5	杨淑华	Journal of Plant Physiology	Senior Editor
6	杨淑华	Stress Biology	Editor
7	杨淑华	Molecular Plant	Advisory Board
8	杨淑华	植物学报	副主编
9	郭 岩	Plant and Cell Physiology	编委
10	郭 岩	Journal of Genetics and Genomics	编委
11	巩志忠	Journal of Integrative Plant Biology	主编
12	王 毅	Journal of Integrative Plant Biology	Editor
13	王 毅	New Phytologist	Advisory Board
14	王 毅	New Crops	Editor
15	王 毅	Science Bulletin	Editor
16	傅 缨	植物学报	编委
17	傅 缨	植物生理学报	编委
18	傅 缨	New Phytologist	Advisory Board
19	傅 缨	Journal of Integrative Plant Biology	编委
20	秦 峰	Molecular Breeding	Associate Editor
21	秦 峰	Trends in Plant Science	Advisory Board
22	秦 峰	Plant Journal	Associate Editor
23	秦 峰	Plant Molecular Breeding	Associate Editor
24	秦 峰	植物学报	责任编辑
25	李继刚	Journal of Integrative Plant Biology	Editor
26	李继刚	Stress Biology	Editor
27	李继刚	New Crops	Associate Editor
28	徐明良	Molecular Breeding	Editor
29	徐明良	Theoretical and Applied Genetics	Editor
30	徐明良	Crop Journal	Editor
31	徐明良	作物学报	副主编
32	徐明良	玉米科学	编委
33	田 丰	Journal of Integrative Plant Biology	Editor
34	田 丰	New Crops	Editor
35	田 丰	Molecular Breeding	Editor
36	田 丰	作物学报	编委
37	田 丰	中国农业科学	编委
38	杨小红	New Crops	Associate Editor
39	田晓莉	Journal of Cotton Research	编委
40	田晓莉	棉花学报	编委
41	陈其军	农业生物技术学报	编委
42	陈其军	BMC Plant Biology	编委
43	陈其军	生物工程学报	编委
44	陈其军	Frontiers in Genome Editing	编委



序号	人员姓名	期刊名称	职务
45	陈其军	New Crops	编委
46	王良省	Frontiers in Plant Science	Reviewer Editor
47	王良省	International Journal of Molecular Sciences	Section Editor
48	王良省	International Journal of Molecular Sciences	编委
49	杨永青	西北植物学报	编委
50	杨永青	农业生物技术学报	编委
51	杨永青	International Journal of Molecular Sciences	编委
52	杨永青	环球生命科学研究	编委
53	于静娟	BMC Plant Biology	编委
54	田长富	Microbial Biotechnology	编委
55	田长富	Journal of Bacteriology	编委
56	田长富	Journal of Systematics and Evolution	编委
57	张永亮	Frontiers in Microbiology	Reviewer Editor
58	张永亮	Molecular Biology Reports	Section Editor
59	张永亮	Crop Health	青年编委
60	蒋才富	Journal of Integrative Plant Biology	编委
61	蒋才富	New Crops	编委
62	张 静	Journal of Integrative Plant Biology	编委
63	张 静	New Crops	编委
64	梁鹏博	aBIOTECH	编委
65	郑绍建	Annals of Botany	地区编委
66	郑绍建	Journal of Integrative Plant Biology	编委
67	刘建祥	BMC Plant Biology	副编辑
68	刘建祥	aBIOTECH	编委
69	刘建祥	Science Bulletin	客座编委
70	寿惠霞	Frontiers in Plant Sciences	编辑
71	寿惠霞	Plant Physiology and Biochemistry	编委
72	寿惠霞	植物生理学报	编委
73	毛传澡	Frontiers in Plant Science	编委



十二、博士后及客座人员

序号	导师	姓名	研究方向	在实验室承担的课题
1	杨淑华	王 西	植物逆境	植物耐低温分子机制研究
2	杨淑华	陶肖蕾	作物主要性状遗传育种	蛋白相互作用验证
3	杨淑华	曾 榕	植物逆境	植物耐低温分子机制研究
4	杨淑华	路晓明	作物遗传育种	蛋白相互作用验证
5	杨淑华	潘巧文	作物主要性状遗传育种	蛋白相互作用验证
6	郭 岩	马 亮	植物逆境	植物耐盐碱基因挖掘
7	郭 岩	刘国永	植物逆境	植物耐盐碱基因挖掘
8	郭 岩	张天任	植物逆境	植物耐盐碱基因挖掘
9	田长富	纪园园	共生固氮	共生固氮机制
10	周文焜	耿 新	植物再生	植物再生分子机制解析
11	李继刚	韩 润	植物逆境	光调控耐盐的分子机制
12	李继刚	彭 晶	植物逆境	光调控ABA信号的分子机制
13	李继刚	冯子懿	植物逆境	phyA信号转导的分子机制
14	李继刚	秦昕妍	植物逆境	光调控ABA信号的分子机制
15	李继刚	段 杰	植物逆境	phyA信号转导的分子机制
16	张永亮	张定谅	植物免疫	植物抗病毒免疫机理解析
17	王良省	赵 欢	植物免疫	叶绿体单线态氧信号转导机理解析
18	王献兵	佟 昕	植物免疫	小肽自噬受体功能研究
19	傅 纓	钟 华	植物细胞生物学	气孔开发机制研究
20	傅 纓	石 磊	植物生殖发育	小孢子母细胞发生调控机制研究
21	傅 纓	李 星	植物生殖发育	植物耐盐机制研究
22	毛同林	邓 佳	植物细胞生物学	微管结合蛋白的功能研究
23	杨小红	张 璇	玉米功能基因组学	玉米产量和品质性状基因挖掘
24	杨小红	赵炳浩	玉米功能基因组学	玉米籽粒含油量分子机理研究
25	杨小红	郭江华	玉米功能基因组学	KRN2分子调控机制和育种应用
26	毕国志	王 攀	植物抗病	植物抗病机制研究
27	徐明良	朱 芒	遗传育种	玉米抗灰斑病抗病机理
28	徐明良	张倩倩	遗传育种	玉米抗丝黑穗病抗病机理
29	徐明良	邓穗宁	遗传育种	玉米抗粗缩病机理
30	毛传澡	朱建树	根构型	根构型
31	毛传澡	李 勇	根构型	根构型
32	毛传澡	任美燕	根构型	根构型
33	毛传澡	蒙福宁	磷信号调控	磷信号调控
34	郑绍建	叶佳园	植物氮营养与逆境适应机制研究	植物缺氮和酸信号感受和应答关键蛋白质的功能与结构解析
35	郑绍建	崔孟奇	植物根毛发育机制研究	植物磷营养
36	郑绍建	徐 晨	植物抗铝机制研究	植物酸铝感知
37	郑绍建	袁俊杰	植物重金属逆境适应机制研究	植物重金属抗性机制
38	刘建祥	张霖霖	植物抗逆	拟南芥响应温和高温的分子机制
39	刘建祥	杨 闯	植物抗逆	水稻耐热的分子机制研究



十三、课题组工作进展



武维华
课题组

武维华，教授，中国科学院院士。教育部重大人才工程特聘教授(1999)，国家杰出青年科学基金获得者(1995)。
研究方向：植物响应低钾、低磷及干旱、高盐胁迫的分子机制研究。

(一) 研究进展

1、光信号调控植物氮、钾养分根冠转运的分子机制

光是调节植物生长发育的重要环境信号，在多种生理活动中发挥重要作用。已有研究表明，光信号可以调控养分的吸收和运输过程。在光照条件下，蒸腾拉力是推动水分和养分由根部向冠部运输的主要动力；而在黑暗中，蒸腾作用减弱，根压则成为主要的运输动力，但光信号调控养分运输的分子机制目前尚不明确。实验室前期研究表明，拟南芥转录因子MYB59.3通过正调控离子转运体基因NPF7.3的转录水平，从而调节K⁺和NO₃⁻向木质部装载，进而影响钾和氮的根冠协同转运。进一步研究发现MYB59.3和NPF7.3的转录水平均在黑暗中升高，而在光下降低。MYB59.3和NPF7.3蛋白也在黑暗中积累，光下降解，说明光信号可以调控MYB59.3和NPF7.3的表达水平。HY5和PIFs是光信号途径中的核心转录因子，HY5和PIF4蛋白分别在光下和暗下的拟南芥根部积累，它们可以直接结合在MYB59.3的启动子区进而调控MYB59.3和NPF7.3的表达。HY5和PIFs分别在白天抑制、夜晚促进MYB59.3-NPF7.3通路，从而调控K⁺和NO₃⁻向根系木质部装载。在光照条件下植物可以借助蒸腾拉力推动水分和养分的根冠运输，HY5蛋白在根中积累抑制MYB59.3-NPF7.3表达，以减少NPF7.3通过消耗跨膜质子梯度介导K⁺和NO₃⁻向木质部主动装载，从而降低能量消耗；黑暗条件下蒸腾拉力减弱，PIFs在根中积累促进MYB59.3-NPF7.3表达，植物通过耗能的方式推动K⁺和NO₃⁻向木质部装载维持木质部汁液渗透压和根压，从而维持夜间水分和养分的根冠运输。该研究结果为阐明光信号调控养分运输的分子机制提供了重要实验证据。相关成果已经于2024年11月被 *New Phytologist* 期刊接收。

Alternating Inverse Modulation of Xylem K⁺/NO₃⁻ Loading by HY5 and PIF Facilitates Diurnal Regulation of Root-to-Shoot Water and Nutrient Transport

Diurnal light/dark cycles regulate nutrient uptake and transport; however, the underlying molecular mechanisms remain largely unknown. Transcription factor MYB59 and ion transporter



NPF7.3 participate in root-to-shoot K^+/NO_3^- translocation in *Arabidopsis*. In this study, transcriptional analyses and Western blotting experiments revealed the diurnal expression of *MYB59-NPF7.3* module. ChIP-qPCR and EMSA showed that transcription factors HY5 and PIFs directly bind to the *MYB59* promoter. Phenotype analyses and ion content measurement indicated that HY5 and PIFs antagonistically control root-to-shoot K^+/NO_3^- translocation through *MYB59-NPF7.3* module. We found HY5 proteins accumulate in root and repress *MYB59* transcription during daytime, while PIFs proteins promote *MYB59* transcription in the dark. By which, the expression levels of *NPF7.3* transcript and protein are gradually decreased during daytime, but increased at night. The enhancement of K^+/NO_3^- loading into the xylem mediated by NPF7.3 could increase root pressure at night, which maintained the root-to-shoot water/nutrient translocation. This study reveals the synergistic mechanism between light signaling and nutrient transport in plants, and defines a diurnal molecular switch of driving forces for root-to-shoot water/nutrient translocation.

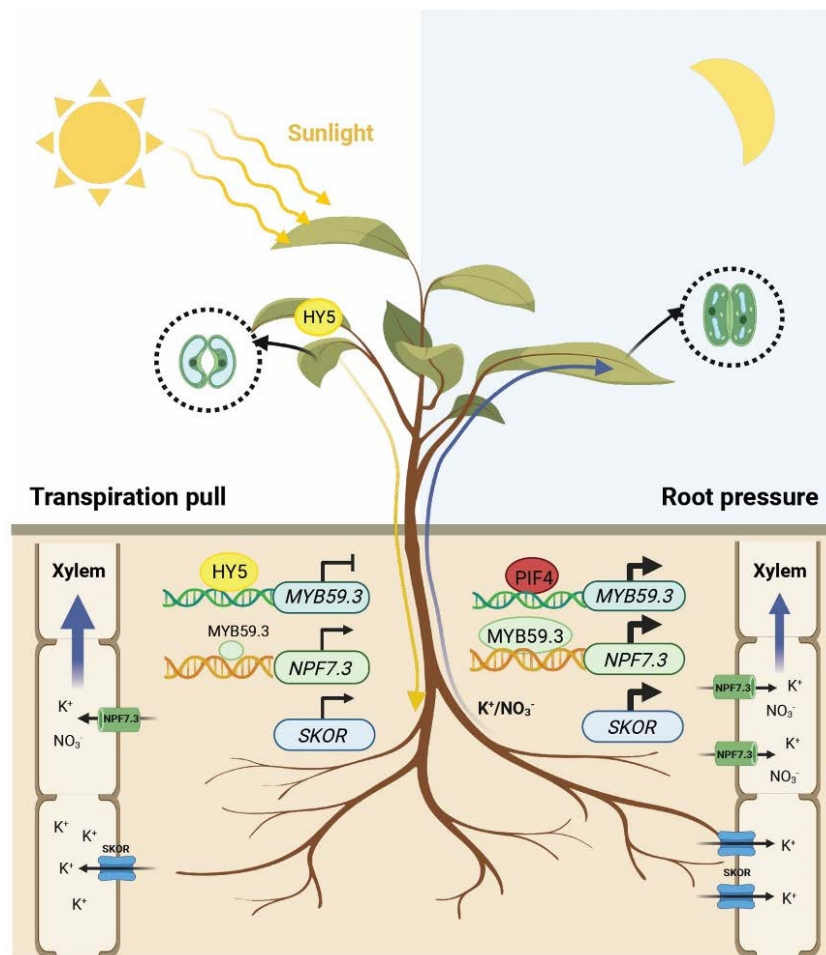


图1、光信号通过转录因子HY5和PIFs调控*MYB59-NPF7.3*模块影响拟南芥氮钾养分根冠转运的模式图。

Figure 1. Working model of *MYB59-NPF7.3* transcriptional regulation by HY5 and PIFs in plant response to the light and dark.



2、CPK28 介导的磷酸化增强了 NRT2.1 在氮剥夺过程中的硝酸盐转运活性

硝酸盐是大多数陆地植物吸收的主要无机氮源形式。植物从土壤中获取硝酸盐依赖一类硝酸盐转运体蛋白(NRTs)，其中NRT2.1是最重要的高亲和性硝酸盐转运体。NRT2.1蛋白活性在各种生理条件下受到复杂的调控，并且NRT2.1具有多个潜在的磷酸化位点。我们发现钙依赖性蛋白激酶28(CPK28)正调控氮剥夺条件下的硝酸盐吸收。通过免疫沉淀和质谱分析，我们发现CPK28与NRT2.1体内互作。随后，利用定量质谱磷酸化蛋白组学技术我们发现了NRT2.1在*cpk28*突变体植物中的磷酸化状态改变异常。通过体外磷酸化实验和磷酸化特异性抗体免疫印迹相结合，我们成功地证明了CPK28特异性地磷酸化NRT2.1的Ser21位点。在爪蟾卵母细胞中进行的功能实验结果显示，CPK28的共表达显著增强了NRT2.1的高亲和性硝酸盐吸收速率。同时，在*nrt2.1*和*cpk28*突变体背景的转基因植株中，在经历氮剥夺过程时，只有表达Ser21位点模拟持续磷酸化状态的蛋白变体NRT2.1^{S21E}完全恢复了突变体的高亲和性硝酸盐吸收能力，而模拟非磷酸化状态的蛋白变体NRT2.1^{S21A}则不能。氮剥夺条件下CPK28自身的激酶活性会增强。这些发现为理解植物在应对变化的硝酸盐需求的复杂调控机制提供了有价值的见解 (Yue et al., *New Phytol*, 2024)。

CPK28-Mediated Phosphorylation Enhances Nitrate Transport Activity of NRT2.1 During Nitrogen Deprivation

Nitrate serves as the primary inorganic nitrogen source assimilated by most terrestrial plants. The acquisition of nitrate from the soil is facilitated by NITRATE TRANSPORTERS (NRTs), with NRT2.1 being the key high-affinity nitrate transporter. The activity of NRT2.1, which has multiple potential phosphorylation sites, is intricately regulated under various physiological conditions. Here, we discovered that CALCIUM-DEPENDENT PROTEIN KINASE 28 (CPK28) positively regulates nitrate uptake under nitrogen deprivation conditions. We found CPK28 as the kinase targeted by immunoprecipitation followed by mass spectrometry and examined the *in-planta* phosphorylation status of NRT2.1 in *cpk28* mutant plants by employing quantitative MS-based phosphoproteomics. Through a combination of *in vitro* phosphorylation experiment and immunoblotting using phospho-specific antibody, we successfully demonstrated that CPK28 specifically phosphorylates NRT2.1 at Ser21. Functional analysis conducted in *Xenopus* oocytes revealed that co-expression of CPK28 significantly enhanced high-affinity nitrate uptake of NRT2.1. Further investigation using transgenic plants showed that the phosphomimic variant NRT2.1^{S21E}, but not the nonphosphorylatable variant NRT2.1^{S21A}, fully restored high-affinity ¹⁵NO₃⁻ uptake ability in both *nrt2.1* and *cpk28* mutant backgrounds. This study clarifies that the kinase activity of CPK28 is promoted during nitrogen deprivation conditions. These significant findings provide valuable insights into the intricate regulatory mechanisms that govern nitrate-demand adaptation (Yue et al., *New Phytol*, 2024).

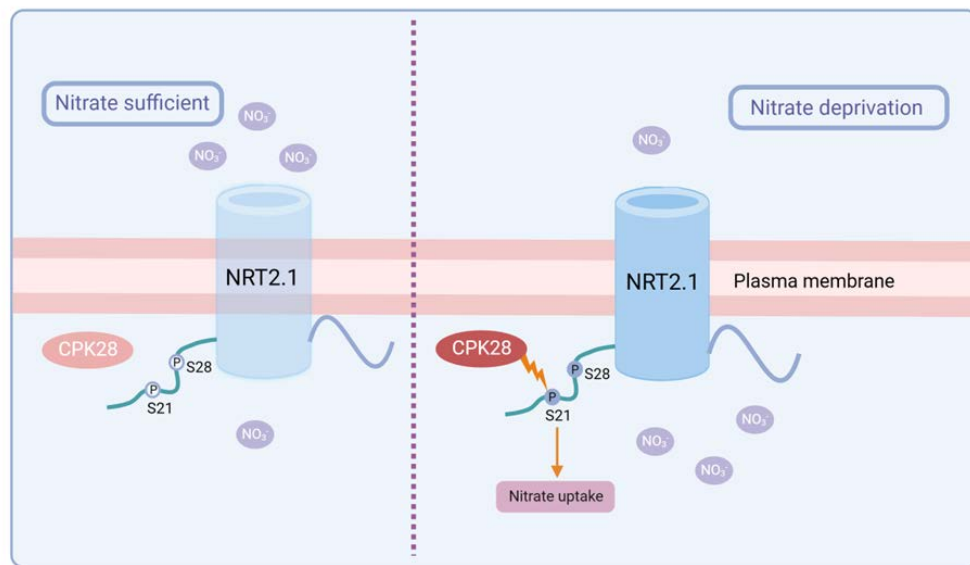


图2、氮剥夺过程中CPK28介导的磷酸化增强了NRT2.1的硝酸盐转运活性。

Figure 2. CPK28-mediated phosphorylation enhances nitrate transport activity of NRT2.1 during nitrogen deprivation.

3、ZmCRK1 调控质膜 H⁺-ATPase 响应玉米干旱胁迫的机制研究

干旱严重影响作物生长和产量。气孔调节在植物对干旱胁迫的响应中起着重要作用。光激活质膜定位的质子 ATP 酶(PM H⁺-ATP 酶)主要促进气孔打开。干旱胁迫下,脱落酸(ABA)在气孔关闭中起主导作用。目前尚不清楚 PM H⁺-ATP 酶如何参与 ABA 诱导的气孔关闭的调节。本实验研究发现钙依赖型蛋白激酶相关激酶的突变体 *zmcrk1* 突变体离体叶片失水慢,对 ABA 诱导的气孔关闭敏感性增加,干旱胁迫再复水后植株存活率高。通过 LCI、BiFC 和 Pull down 实验结果显示 ZmCRK1 与玉米 PM H⁺-ATP 酶 ZmMHA2 和 ZmMHA3 的全长在细胞膜上互作,ZmCRK1 磷酸化 ZmMHA2 C 端的 Ser-901,抑制其质子泵活性。ABA 瞬时激活质膜 H⁺-ATPase,导致保卫细胞外向 H⁺流速增大,然而 *ZmCRK1* 过表达株系和 *zmmha2* 突变体中 ABA 诱导的 H⁺外排减弱,*zmcrk1* 突变体的 H⁺-ATPase 活性在正常条件下显著高于野生型,ABA 处理后保卫细胞的 H⁺外排速率略大于野生型。*zmmha2* 突变体离体叶片失水快,对 ABA 诱导的气孔关闭敏感性降低,干旱胁迫再复水后植株存活率低。本研究发现了在干旱胁迫下调控质膜 H⁺-ATPase 活性的蛋白激酶 ZmCRK1。在水分充足条件下,ZmCRK1 磷酸化 ZmMHA2 抑制其活性,使保卫细胞 H⁺外排减少,气孔打开,维持植物的正常生长。在干旱条件下,ZmCRK1 蛋白减少,削弱其对 ZmMHA2 的抑制作用,H⁺外排增加,从而导致气孔关闭,以适应干旱胁迫 (Liu et al., *New Phytol*, 2024)。

ZmCRK1 Negatively Regulates Maize's Response to Drought Stress by Phosphorylating Plasma Membrane H⁺-Atpase ZmMHA2

Drought severely affects crop growth and yields. Stomatal regulation plays an important role in plant response to drought stress. Light-activated plasma membrane-localized proton ATPase

(PM H⁺-ATPase) mainly promoted the stomatal opening. Abscisic acid (ABA) plays a dominant role in the stomatal closure during drought stress. It's not clear how PM H⁺-ATPase is involved in the regulation of ABA-induced stomatal closure. We found that a CALCIUM-DEPENDENT PROTEIN KINASE RELATED KINASE 1 (ZmCRK1), and its mutant *zmcrk1* exhibited slow water loss in detached leaves, high survival rate after drought stress, and sensitivity to stomatal closure induced by ABA. The *ZmCRK1* overexpression lines are opposite. ZmCRK1 interacted with the maize PM H⁺-ATPase ZmMHA2. ZmCRK1 phosphorylated ZmMHA2 at the Ser-901 and inhibited its proton pump activity. *ZmCRK1* overexpression lines and *zmmha2* mutants had low H⁺-ATPase activity, resulting in impaired ABA-induced H⁺ efflux. Taken together, our study indicates that ZmCRK1 negatively regulates maize drought stress response by inhibiting the activity of ZmMHA2. Reducing the expression level of *ZmCRK1* has the potential to reduce yield losses under water deficiency (Liu et al., *New Phytol*, 2024).

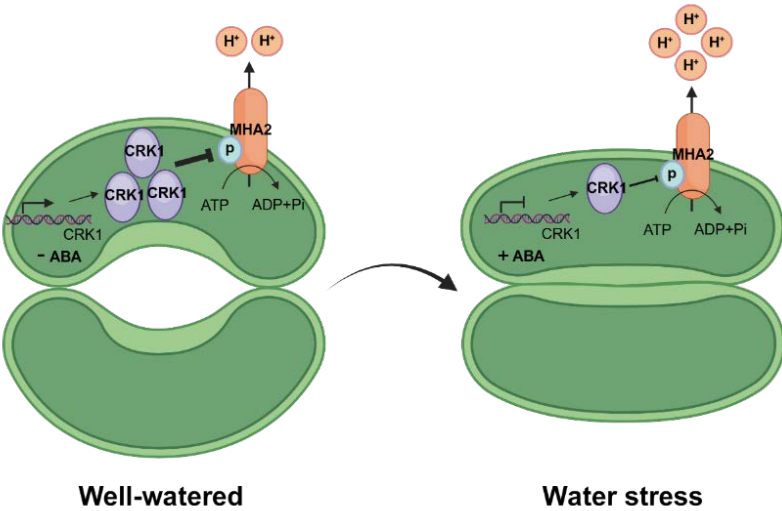


图3、ZmCRK1调控玉米ZmMHA2活性的作用机制模型。
Figure 3. Working model of ZmMHA2 activity modulation mediated by ZmCRK1 under well-watered and drought conditions.

4、玉米 ZmPHR1 协同调控磷素利用和水分胁迫的分子机制

磷是一种必需的大量矿质元素，由于有效磷在土壤中的浓度极低且移动性差，磷通常是一种限制性必需营养元素。干旱是造成作物减产的主要环境胁迫。植物如何平衡磷素饥饿反应(PSR)和耐受水分胁迫的机制尚不清楚。我们研究发现，转录因子 ZmPHR1 是调节 PSRs 的关键因子。玉米 *zmphr1* 突变体的磷含量降低，对低磷胁迫敏感，而 *zmphr1* OE 株系的磷含量和产量都增加。此外，叶片中 57% 的 PSR 基因和近 70% 的 ZmPHR1 调控 PSR 基因响应干旱胁迫。在中度干旱的早期，玉米的无机磷含量降低，PSR 基因的表达上调先于干旱胁迫响应基因。ZmPHR1 OE 株系表现出抗旱表型和气孔孔径减小，而 *zmphr1* 突变体则相反。为了进一步验证植物磷素稳态与水分胁迫耐受之间的关联性，选择磷含量有差异的玉米遗传材料进行实验，发现无机磷含量升高的 *ZmPT7* OE 株系和



zmspx3 突变体也表现出抗旱性，但无机磷含量降低的 *zmpt7* 突变体对干旱敏感。该研究揭示，ZmPHR1 在整合 Pi 和干旱信号方面起着核心作用，磷稳态的维持提高了玉米抗旱能力。研究工作为挖掘调控玉米营养高效和环境广适的关键基因提供新思路，主要研究结果发表在 *Plant Biotechnol J* (Tian et al., 2024)。

ZmPHR1 Contributes to Drought Resistance by Modulating Phosphate Homeostasis in Maize

As an essential macronutrient, phosphorus (P) is often a limiting nutrient because of its low availability and mobility in soils. Drought is a major environmental stress that reduces crop yield. How plants balance and combine P-starvation responses (PSRs) and drought resistance is unclear. In this study, we identified the transcription factor ZmPHR1 as a major regulator of PSRs that modulates phosphate (Pi) signaling and homeostasis. We found that maize *zmphr1* mutants had reduced P concentration and were sensitive to Pi starvation, whereas *ZmPHR1-OE* lines displayed elevated Pi concentration and yields. In addition, 57% of PSR genes and nearly 70% of ZmPHR1-regulated PSR genes in leaves were transcriptionally responsive to drought. Under moderate and early drought conditions, the Pi concentration of maize decreased, and PSR genes were up-regulated before drought-responsive genes. The *ZmPHR1-OE* lines exhibited drought-resistant phenotypes and reduced stomatal apertures, whereas the opposite was true of the *zmphr1* mutants. *ZmPT7-OE* lines and *zmspx3* mutants, which had elevated Pi concentration, also exhibited drought resistance, but *zmpt7* mutants were sensitive to drought. Our results suggest that ZmPHR1 plays a central role in integrating Pi and drought signals and that Pi homeostasis improves the ability of maize to combat drought (Tian et al., *Plant Biotechnol J*, 2024).

5、综述玉米磷营养的分子和遗传调控机制

磷是植物必需的矿质营养元素，影响植物/作物的生长发育和产量。植物主要通过根系吸收土壤中的有效磷(无机磷)。土壤中的无机磷容易被固定或形成植物不能吸收的有机磷，因此土壤中的无机磷常常缺乏，抑制植物/作物的生长发育，造成作物减产。为了适应环境磷素缺乏，植物进化出一系列应对措施和机制。玉米是世界广泛种植的主要谷类作物，提高其磷利用效率对于保障玉米生产至关重要。在过去的二十年里，旨在使玉米品种适应环境磷供应变化的研究取得了相当大的进展。我们综述了玉米的磷吸收、转运和再分配的生理和分子机制，并整合了拟南芥和水稻的磷素营养研究进展。此外，我们还总结了磷素营养与非生物胁迫应答之间的关联性。解析玉米磷素吸收和利用的分子机制可以为实现可持续农业生产提供理论依据 (Guo et al., *J Genet Genomics*, 2024)。

Phosphorus Acquisition, Translocation, and Redistribution in Maize

Phosphorus (P) is an essential nutrient for crop growth, making it important for maintaining food security as the global population continues to increase. Plants acquire P primarily via the



uptake of inorganic phosphate (Pi) in soil through their roots. Pi, which is usually sequestered in soils, is not easily absorbed by plants and represses plant growth. Plants have developed a series of mechanisms to cope with P deficiency. Moreover, P fertilizer applications are critical for maximizing crop yield. Maize is a major cereal crop cultivated worldwide. Increasing its P-use efficiency is important for optimizing maize production. Over the past two decades, considerable progresses have been achieved in research aimed at adapting maize varieties to changes in environmental P supply. Here, we present an overview of the morphological, physiological, and molecular mechanisms involved in P acquisition, translocation, and redistribution in maize and combine the advances in *Arabidopsis* and rice, to better elucidate the progress of P nutrition. Additionally, we summarize the correlation between P and abiotic stress responses. Clarifying the mechanisms relevant to improving P absorption and use in maize can guide future research on sustainable agriculture (Guo et al., *J Genet Genomics*, 2024).

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Jing S, Zhang H, Yang Z, Du X, Hu Y, Wang S, Wang S, Zhang K, Li Z, Wu W, Kudla J, Li J, Wang Y* (2024) Alternating inverse modulation of xylem K^+/NO_3^- loading by HY5 and PIF facilitates diurnal regulation of root-to-shoot water and nutrient transport. **New Phytol** DOI: 10.1111/nph.20319.
2. Yue L#, Liu M#, Liao J, Zhang K, Wu W, Wang Y* (2024) CPK28-mediated phosphorylation enhances nitrate transport activity of NRT2.1 during nitrogen deprivation. **New Phytol** DOI: 10.1111/nph.20236.
3. Liu J#, Li X#, Jia D, Qi L, Jing R, Hao J, Wang Z, Cheng J, Chen L* (2024) ZmCRK1 negatively regulates maize's response to drought stress by phosphorylating plasma membrane H^+ -ATPase ZmMHA2. **New Phytol** 244: 1362-1376.
4. Tian M#, Wang H#, Tian Y#, Hao J#, Guo H, Chen L, Wei Y, Zhan S, Yu H, Chen Y* (2024) ZmPHR1 contributes to drought resistance by modulating phosphate homeostasis in maize. **Plant Biotechnol J** 22: 3085-3098.
5. Guo H#, Tian M#, Ri X, Chen Y* (2024) Phosphorus acquisition, translocation, and redistribution in maize. **J Genet Genomics** DOI: 10.1016/j.jgg.2024.09.018.

专利授权:

1. 王毅, 武维华, 姬赟, 韩武, 王喜庆, 陈丽梅, 赵晓明: 一种玉米抗倒伏基因及其相关蛋白和生物材料的应用; 专利号: ZL 202310720864.X; 授权公告日: 2024 年 06 月 28 日。



2. 张帅松, 陈丽梅, 李建生, 贾冬云; 一种玉米耐高温评价的方法; 专利号: ZL 202310592286.6;
授权公告日: 2024 年 02 月 20 日。
3. 王喜庆, 庄军红, 赵晓明, 陈丽梅; 矮 20 蛋白、其编码基因及应用; 专利号: ZL 202110324876.1;
授权公告日: 2024 年 06 月 21 日。

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研究方向：植物感受与应答温度（低温和高温）胁迫的分子机制。

(一) 研究进展

1、热休克转录因子 HSF21 调控玉米耐冷性的分子机制

玉米 (*Zea mays* L.) 是一种起源于热带的粮食作物，对低温胁迫十分敏感，我国玉米主产区经常遭受低温寒害的影响，极大威胁了玉米的生长发育及其产量，因此，研究玉米耐冷性的分子机制以及挖掘有效的自然变异，可以为培育耐冷玉米提供基因资源和分子理论基础，对提高作物的适应性和生产力、缓解极端温度造成的作物减产具有重要意义。我们通过统计玉米自然群体中不同纬度来源的 213 份玉米自交系在低温处理后的叶片相对损伤面积，利用全基因组关联分析的方法，鉴定出与玉米冷表型最显著关联的 SNP 位于候选基因 *HSF21* 的启动子区。*HSF21* 过表达株系在玉米萌发期和苗期都具有很强的耐冷性，而 *hsf21* 突变体植株无论是萌发期还是苗期都表现出对低温敏感的表现。通过重测序，发现 *HSF21* 启动子区的一个 SNP (-683) 和一个 InDel5 (-693) 的自然变异与玉米自交系耐冷性显著相关，并且这两个自然变异位点高度连锁，根据二者的区别可以将玉米自交系划分为 Hap1、Hap2 和 Hap3 三种单倍型，其中 Hap1 型玉米自交系为优势单倍型，对应的等位基因 *HSF21*^{Hap1} 为优势等位基因。进一步研究表明，等位基因 *HSF21*^{Hap1} 启动子区的自然变异导致了一个典型的 A-box (5'-TACGTA-3') 基序的丢失，从而削弱了玉米耐冷性负调节因子 bZIP68 对其的转录抑制作用，使得等位基因 *HSF21*^{Hap1} 低温诱导表达，从而正调控玉米耐冷性。通过联合 RNA-seq 和 DAP-seq 分析发现 HSF21 直接调节玉米重要脂代谢基因的表达水平从而调控玉米低温下脂代谢过程，进一步结合高通量的玉米脂质组分析揭示 HSF21 是调控玉米低温胁迫下脂代谢稳态的关键基因，控制着低温下不饱和脂质的代谢平衡，证实 HSF21 正调控玉米耐冷性是通过维持玉米低温胁迫下脂代谢稳态来实现的。最后，我们发现过表达 *HSF21* 不仅能够增强玉米耐冷性，还能够显著提高玉米田间产量。该研究通过正向遗传学鉴定一个关键的玉米耐低温基因 *HSF21*，为培育耐冷高产玉米提供了理论依据和新的基因资源 (Gao et al., *Mol Plant*, 2024)。

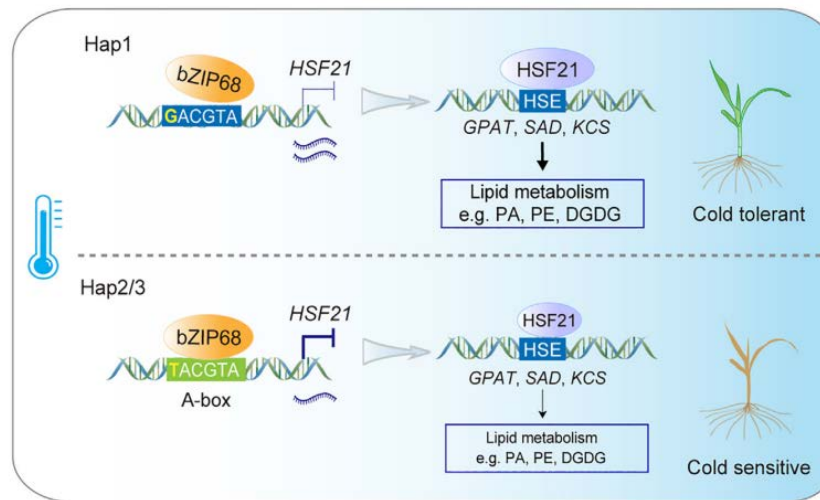


图1、HSF21增强玉米耐冷性的分子机制模型。

Figure 1. A working model illustrating how HSF21 promotes cold tolerance in maize.

Genetic Variation in a Heat Shock Transcription Factor HSF21 Modulates Cold Tolerance in Maize

Understanding how maize (*Zea mays*) responds to cold stress is crucial for facilitating breeding programs of cold-tolerant varieties. Despite extensive utilization of the genome-wide association study (GWAS) approach for exploring favorable natural alleles associated with maize cold tolerance, few studies have successfully identified candidate genes that contribute to maize cold tolerance. In this study, we used a diverse panel of inbred maize lines collected from different germplasm sources to perform a GWAS on variations in the relative injured area of maize true leaves during cold stress—a trait very closely correlated with maize cold tolerance. We identified *HSF21*, which encodes a B-class heat shock transcription factor (HSF) that positively regulates cold tolerance at both the seedling and germination stages. Natural variations in the promoter of the cold-tolerant *HSF21*^{Hap1} allele led to increased *HSF21* expression under cold stress by inhibiting binding of the basic leucine zipper bZIP68 transcription factor, a negative regulator of cold tolerance. By integrating transcriptome deep sequencing, DNA affinity purification sequencing, and targeted lipidomic analysis, we revealed the function of *HSF21* in regulating lipid metabolism homeostasis to modulate cold tolerance in maize. In addition, we found that *HSF21* confers maize cold tolerance without incurring yield penalties. Collectively, this study establishes *HSF21* as a key regulator that enhances cold tolerance in maize, providing valuable genetic resources for breeding of cold-tolerant maize varieties (Gao et al., *Mol Plant*, 2024).

2、CNGC20 钙离子通道差异磷酸化调控钙信号介导的植物抗冻性的分子机制

钙离子(Ca^{2+})作为重要的第二信使, 不仅调控植物多个生长发育过程, 而且还参与植物对逆境的响应。不同类型的环境胁迫会引起细胞内钙离子浓度的特定变化模式。低温胁迫诱导细胞质钙离子



浓度 $[Ca^{2+}]_{cyt}$ 瞬间升高，从而启动特异钙信号。然而，过高的 Ca^{2+} 对植物会造成毒害，因此细胞内的 Ca^{2+} 浓度需要被严格控制。我们研究发现钙离子通道 *CNGC20* 功能缺失突变体具有低温敏感表型，而 *CNGC20* 过表达植株表现为耐冻表型；*CNGC20* 基因的缺失导致低温诱导的 $[Ca^{2+}]_{cyt}$ 、低温响应关键转录因子 *CBFs* 的基因表达均降低，证明 *CNGC20* 通过介导低温诱导的 $[Ca^{2+}]_{cyt}$ 正调控拟南芥的耐冻性。进一步研究发现在低温胁迫的早期，类受体激酶 *PSY1R* 被低温激活，通过磷酸化 *CNGC20* 增强其通道活性，正调控植物耐冻性；而在长期低温胁迫中，低温信号的负调控因子胞质类受体激酶 *CRPK1* 通过磷酸化 *CNGC20*，促进其在低温下的降解，减弱植物对低温胁迫的响应。该研究揭示了两类激酶对钙离子通道 *CNGC20* 不同位点的磷酸化，实现对通道活性和蛋白稳定性的调节，从而精细调控植物低温应答的分子机制，为理解植物如何适应低温胁迫提供了理论依据 (Peng et al., *Plant Cell*, 2024)。

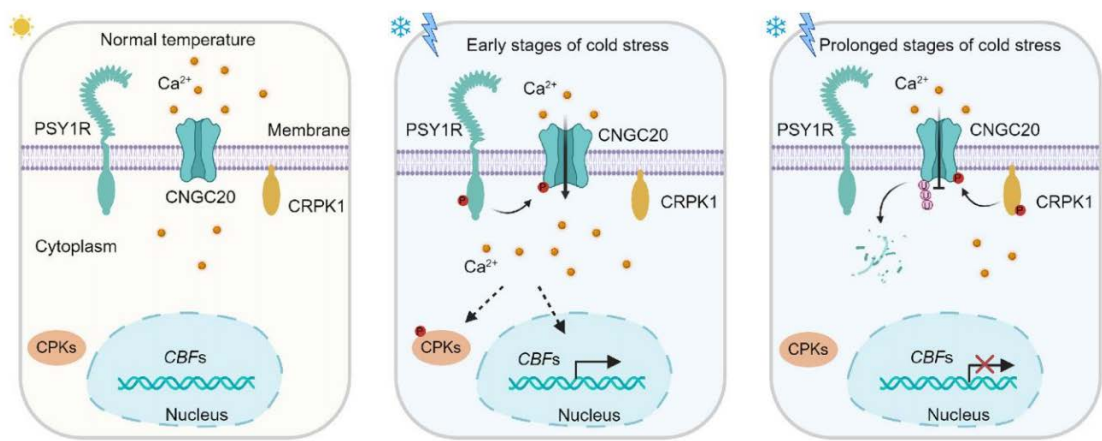


图2、PSY1R-CRPK1-CNGC20调控植物响应低温胁迫的分子模型。

Figure 2. A proposed working model for the function of PSY1R-CRPK1-CNGC20 in modulating freezing tolerance in *Arabidopsis*.

Differential Phosphorylation of CNGC20 Antagonistically Modulates Calcium-Mediated Freezing Tolerance in *Arabidopsis*

Plants respond to cold stress at multiple levels, including increasing cytosolic calcium (Ca^{2+}) influx and triggering the expression of cold-responsive genes. In this study, we show that the Ca^{2+} -permeable channel CYCLIC NUCLEOTIDE-GATED CHANNEL20 (*CNGC20*) positively regulates freezing tolerance in *Arabidopsis* (*Arabidopsis thaliana*) by mediating cold-induced Ca^{2+} influx. Moreover, we demonstrate that the leucine-rich repeat receptor-like kinase PLANT PEPTIDE CONTAINING SULFATED TYROSINE1 RECEPTOR (*PSY1R*) is activated by cold, phosphorylating and enhancing the activity of *CNGC20*. The *psy1r* mutant exhibits decreased cold-evoked Ca^{2+} influx and freezing tolerance. Conversely, COLD-RESPONSIVE PROTEIN KINASE1 (*CRPK1*), a protein kinase that negatively regulates cold signaling, phosphorylates and facilitates the degradation of *CNGC20* under prolonged periods of cold treatment, thereby attenuating



freezing tolerance. This study thus identifies PSY1R and CRPK1 kinases that regulate CNGC20 activity and stability, respectively, thereby antagonistically modulating freezing tolerance in plants (Peng et al., *Plant Cell*, 2024).

3、液泡膜水通道蛋白 *TIP4;3* 基因的自然变异调控玉米耐冷性

玉米 (*Zea mays* L.) 作为全球重要的粮食作物，原产于热带地区，对低温的敏感性制约了其在高纬度地区的种植范围和产量品质。本研究通过反向遗传学筛选的方法，发现过表达 *TIP2;1*、*TIP3;2*、*TIP4;3* 等液泡膜水通道蛋白基因显著降低玉米的耐冷性。利用 CRISPR/Cas9 技术构建的 *tip4;3* 突变体，在萌发期和苗期均表型出耐冷性显著增强，表明 TIPs 家族成员在玉米耐冷性中起重要的负调控作用。值得注意的是，*TIP4;3* 基因在不同玉米自交系中的表达水平呈现显著差异。通过候选基因关联分析发现，*TIP4;3* 基因启动子区域中存在一个 CACTA 类型转座子的插入或缺失的自然变异，影响组蛋白 H3K37me3 和 H3K9me2 的修饰水平，从而导致 *TIP4;3* 表达水平及玉米耐冷性的差异。进一步研究显示，*TIP4;3* 通过调控低温胁迫下的气孔运动、活性氧(ROS)的积累以及冷响应(*COR*)基因的表达，负向调控玉米的耐冷性 (图 3)。综上，该研究不仅揭示了液泡膜水通道蛋白 *TIP4;3* 在调控玉米耐冷性的分子机制，还为培育耐冷性增强的玉米新种质提供了理论基础和重要基因资源 (Zeng et al., *Plant Biotechnol J*, 2024)。

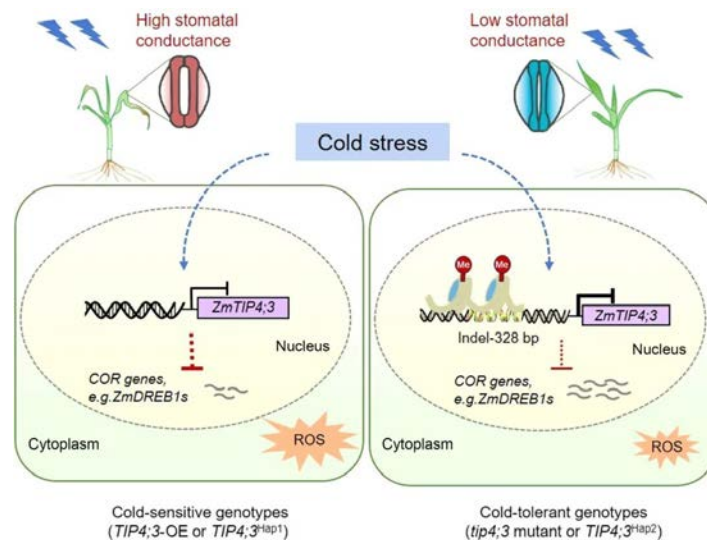


图 3、*TIP4;3* 调控玉米耐冷性的机制模型。

Figure 3. Model of *TIP4;3*-mediated cold tolerance in maize.

Genetic Variation in the Aquaporin TONOPLAST INTRINSIC PROTEIN 4;3 Modulates Cold Tolerance in Maize

Cold stress is a major abiotic stress that threatens maize (*Zea mays* L.) production worldwide. Tonoplast intrinsic proteins (TIPs) are a subfamily of aquaporins in plants. Here, we report that TIP family proteins are involved in maize cold tolerance. The expression of most TIP genes was responsive to cold stress. Overexpressing *TIP2;1*, *TIP3;2* or *TIP4;3* reduced the cold tolerance of



maize seedlings, while loss-of-function mutants of *TIP4;3* exhibited enhanced cold tolerance, suggesting that *TIP4;3* play a crucial roles in negatively regulate maize cold tolerance.. Notably, candidate gene association analysis revealed that natural variations involving the insertion or deletion of a CACTA-type transposon in the promoter region of *TIP4;3* influence histone modification levels, specifically H3K37me3 and H3K9me2. These epigenetic changes lead to differences in *TIP4;3* expression and cold tolerance in maize. Further studies showed that *TIP4;3* negatively regulates maize cold tolerance by modulating stomatal movement, reactive oxygen species (ROS) accumulation. This study thus elucidates the mechanism underlying TIP-mediated cold tolerance and identifies a favourable *TIP4;3* allele as a potential genetic resource for breeding cold-tolerant maize varieties (Zeng et al., *Plant Biotechnol J*, 2024).

4、脂代谢调控玉米耐冷性的重要功能

当植物受到低温胁迫时，细胞膜脂质组成会发生显著改变，并且这种生理上的改变可能与植物低温应答过程关系密切。我们研究发现，低温胁迫诱导的玉米脂质重塑过程具有选择性和特异性。以糖脂 MGDG 和磷脂 PC 为例，低温胁迫下 MGDG 36:5 和 PC 34:2 的含量显著降低，而 MGDG36:6 和 PC36:4 的含量无明显改变。在磷脂 PA 和甘油酯 DAG 中，PA36:5、PA36:6、DAG36:5 和 DAG36:6 的含量呈现特异受低温诱导的变化趋势。这些低温下特异变化的脂质化合物可以被开发成为脂质组 GWAS 的分子标记，有助于为开发玉米耐寒品系挖掘基因资源。此外，低温胁迫显著诱导磷脂 PA 和 PC 含量的变化，这一现象在不同植物物种中具有保守性。玉米磷脂 PI 含量较低，且受低温胁迫诱导后进一步显著降低，而在拟南芥中并未观察到这一现象，推测磷脂 PI 的含量可能影响着不同植物的耐冷性。综上所述，本研究通过脂质组和遗传分析，有助于全面认识玉米脂代谢和耐冷性之间的内在联系，为作物耐寒性遗传改良挖掘基因资源提供潜在的分子标记和新的研究思路 (Gao et al., *J Genet Genomics*, 2024)。

Genetic and Lipidomic Analyses Reveal the Key Role of Lipid Metabolism for Cold Tolerance in Maize

Lipid remodeling is crucial for cold tolerance in plants. However, the precise alternations of lipidomics during cold responses remain elusive, especially in maize (*Zea mays* L.). Here, we find that the homeostasis of cellular lipid metabolism is essential for maintaining cold tolerance of maize. Under cold stress, the levels of glycolipid MGDG 36:5 and phospholipid PC 34:2 significantly decrease, whereas the levels of MGDG 36:6 and PC 36:4 remain largely unchanged. Regarding phospholipid PA and glycerolipid DAG species, the levels of PA 36:5, PA 36:6, DAG 36:5, and DAG 36:6 show induced by cold stress. Additionally, cold stress induced changes in the levels of phospholipids PA and PC appears to be conserved across different plant species. Thus, these lipids could potentially serve as molecular markers for lipidomics-based GWAS, supporting the identification of genetic resources for developing cold-tolerant maize lines. In summary, these results reveal a comprehensive lipidomic profile during the cold response of maize and provide



genetic resources for enhancing cold tolerance in crops (Gao et al., *J Genet Genomics*, 2024).

5、综述植物耐低温的分子调控机制

随着全球气候改变，极端低温天气频发，严重威胁世界粮食安全。近年来，低温胁迫机理研究取得了较大进展，植物应答低温胁迫的分子调控网络日益清晰。我们应邀在综合期刊 *Annu Rev Genet* 杂志撰写题为“Regulatory Networks Underlying Plant Responses and Adaptation to Cold Stress”的综述文章。该综述通过不同的角度系统总结植物如何在低温胁迫条件下生存和生长。主要包括以下几个部分：(一) 低温胁迫信号的感知和转导通路。本章节深入阐述了植物感知低温信号的机制以及植物感知领域亟需解决的科学问题。同时，本章节着重阐述了近年来发现的重要低温胁迫调节蛋白的作用机制。(二) 低温胁迫信号与其它信号通路的交叉。本章节着重阐述低温胁迫信号与光信号、生物钟、植物激素以及植物免疫之间的关系。(三) 长期低温胁迫对植物生长和开花的影响。本章节阐述了长期低温环境抑制植物的生长和开花的分子机理。(四) 未来方向。本章节提出低温胁迫领域面临的挑战和存在的开放性问题，为该领域今后的研究指出新的思路 (Ding et al., *Annu Rev Genet*, 2024)。

Regulatory Networks Underlying Plant Responses and Adaptation to Cold Stress

Cold is a key determinant for plant growth and flowering time as well as an important environmental factor limiting plant growth and development. Recent studies have revealed the complex regulatory networks associated with plant responses to cold and identified their interconnections with signaling pathways related to light, the circadian clock, plant hormones, and pathogen defense. In this article, we review recent advances in understanding the molecular basis of cold perception and signal transduction pathways. We also summarize recent developments in the study of cold-responsive growth and flowering. Finally, we propose future directions for the study of longterm cold sensing, RNA secondary structures in response to cold, and the development of cold-tolerant and high-yield crops (Ding et al., *Annu Rev Genet*, 2024).

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

1. Gao L[#], Pan L[#], Shi Y^{**}, Zeng R, Li M, Zhang X, Zhao X, Gong X, Huang W, Yang X, Lai J, Zuo J, Gong Z, Wang X, Jin W, Dong Z^{*}, Yang S^{*} (2024) Genetic variation in a heat shock transcription factor modulates cold tolerance in maize. *Mol Plant* 17: 1423-1438.
2. Peng Y[#], Ming Y[#], Jiang B, Zhang X, Lin Q, Zhang X, Wang Y, Shi Y, Gong Z, Ding Y, Yang S^{*} (2024) Differential phosphorylation of CNGC20 antagonistically modulates calcium-mediated



- freezing tolerance in *Arabidopsis*. **Plant Cell** 36: 4356-4371.
3. Ding Y[#], Shi Y[#], Yang S^{*} (2024) Regulatory networks underlying plant responses and adaptation to cold stress. **Annu Rev Genet** DOI: 10.1146/annurev-genet-111523-102226.
 4. Zeng R[#], Zhang X[#], Song G, Lv Q, Li M, Fu D, Zhang Z, Gao L, Zhang S, Yang X, Tian F, Yang S, Shi Y^{*} (2024) Genetic variation in the aquaporin TONOPLAST INTRINSIC PROTEIN 4;3 modulates maize cold tolerance. **Plant Biotechnol J** 22: 3037-3050.
 5. Gao L, Jiang H, Li M, Wang D, Xiang H, Zeng R, Chen L, Zhang X, Zuo J, Yang S, Shi Y (2024) Genetic and lipidomic analyses reveal the key role of lipid metabolism for cold tolerance in maize. **J Genet Genomics** 51: 326-337.
 6. Jing T[#], Wu Y[#], Yu Y, Li J, Mu X, Xu L, Wang X, Qi G, Tang J, Wang D, Yang S, Hua J^{*}, Gou M^{*} (2024) Copine proteins are required for brassinosteroid signaling in maize and *Arabidopsis*. **Nat Commun** 15: 2028.
 7. Liu C[#], Li Q[#], Shen Z, Xia R, Chen Q, Li X, Ding Y, Yang S, Serino G, Xie Q, Yu F^{*} (2024) The *Arabidopsis* E3 ubiquitin ligase DOA10A promotes localization of abscisic acid (ABA) receptors to the membrane through mono-ubiquitination in ABA signaling. **New Phytol** DOI: 10.1111/nph.2024.
 8. Wang Y, Cheng J, Guo Y, Li Z, Yang S, Wang Y^{*}, Gong Z (2024) Phosphorylation of ZmAL14 by ZmSnRK2.2 regulates drought resistance through derepressing *ZmROP8* expression. **J Integr Plant Biol** 66: 1334-1350.
 9. Hu X, Cheng J, Lu M, Fang T, Zhu Y, Li Z, Wang X, Wang Y, Guo Y, Yang S, Gong Z^{*} (2024) Ca²⁺-independent ZmCPK2 is inhibited by Ca²⁺-dependent ZmCPK17 during drought response in maize. **J Integr Plant Biol** 66: 1313-1333.

专利授权:

施怡婷, 杨淑华, 李卓洋; ZmMAPK 蛋白及其编码基因在调控植物低温胁迫耐性中的应用; 专利号: ZL202011565861.6; 授权公告日: 2024.03.19。

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研究方向: 植物感受与响应盐碱胁迫信号的
分子机制。

(一) 研究进展

1、细胞内铵态氮稳态参与调控植物抗盐的分子机制研究

土壤盐碱化对农业和植物生长构成严重威胁。在高盐度条件下, 由于硝化作用受到限制, 铵态氮(NH_4^+)是植物利用的主要无机氮源。然而, 铵如何影响植物对盐胁迫的反应仍然知之甚少。我们发现相比硝态氮(NO_3^-), 铵态氮能增强南芥幼苗对盐胁迫的抵抗力, 且这一反应是由铵转运体(AMTs)介导的。我们进一步证明 SOS2 通过直接磷酸化 AMT1;1 的 C 端非保守区域的丝氨酸残基 Ser-450 并激活 AMT1;1。研究进一步发现盐胁迫下生长的 SOS2 突变体的铵吸收速率比野生型低。此外, AMTs 介导的铵吸收可以进一步增强盐诱导的 SOS2 激酶活性。总之, 我们的研究表明, SOS2 通过磷酸化 AMT1;1 精细调控氨转运体活性并维持盐胁迫下的铵吸收, 以此优化植物的盐胁迫响应 (Ma et al., *Plant Cell*, 2024. Under review)。

The SOS2-AMT1;1 Module Contributes to Plant Salt Tolerance by Maintaining Ammonium Uptake

Soil salinity is a severe threat to agriculture and plant growth. Under high salinity conditions, ammonium (NH_4^+) is the predominant inorganic nitrogen source used by plants due to the limited nitrification. However, how ammonium shapes the plant response to salt stress remains a mystery. Here, we demonstrate that the growth of *Arabidopsis* (*Arabidopsis thaliana*) seedlings is less sensitive to salt stress when provided with ammonium instead of nitrate (NO_3^-), a response that is mediated by ammonium transporters (AMTs). We further show that the kinase SALT OVERLY SENSITIVE2 (SOS2) physically interacts with and activates AMT1;1 by directly phosphorylating the non-conserved serine residue Ser-450 in the C-terminal region. In agreement with the involvement of SOS2, ammonium uptake was lower in *sos2* mutants grown under salt stress relative to the wild type. Moreover, AMT-mediated ammonium uptake enhanced salt-induced SOS2 kinase activity. Together, our study demonstrates that SOS2 activates AMT1;1 to fine-tune and maintain ammonium uptake and optimize the plant salt stress response (Ma et al., *Plant Cell*, 2024. Under review).



2、液泡动态变化调控植物耐盐性的分子机制研究

盐胁迫会导致植物细胞中的离子毒性,从而限制植物的生长和作物的生产力。在盐胁迫条件下,钠离子(Na^+)可以通过运输系统排出细胞外或者被运输到液泡中进行隔离。盐分排泄系统由 SALT OVERLY SENSITIVE (SOS)信号通路控制,该通路包括钙传感器 SOS3 和 SCaBP8、蛋白激酶 SOS2 以及质膜 Na^+/H^+ 反向转运体 SOS1。尽管在分子水平上已对植物的盐胁迫响应有了较深入的了解,但植物是否以及如何通过内膜系统重塑来响应盐胁迫仍不清楚。我们的研究揭示了一种涉及 FREE1 水平调控的盐胁迫耐受机制,该机制影响多泡体(MVB)的运输过程。具体来说,作为 ESCRT-I 组成部分的 FREE1 通过调控液泡碎裂增强了植物的盐胁迫耐受性。SOS2 可对 FREE1 进行磷酸化修饰,促进其降解,从而影响 MVB 的成熟过程,减少 MVB 与液泡的融合,并调节内膜系统动力学以响应盐胁迫。这些发现突出了植物内膜系统在应对盐胁迫中的适应性作用 (Liu et al., *Plant Cell*, 2024. In press)。

Salt stress causes ion toxicity in plant cells and limits plant growth and crop productivity. Sodium ions (Na^+) are transported out of the cell and sequestered in the vacuole for detoxification under salt stress. The salt excretion system is controlled by the SALT OVERLY SENSITIVE (SOS) pathway, which consists of the calcium sensors SOS3 and SOS3-LIKE CALCIUM BINDING PROTEIN 8, the protein kinase SOS2, and the plasma membrane Na^+/H^+ antiporter SOS1. Although much is known about salt responses in plants at the molecular level, it remains unclear if and how plants respond to salt stress through endomembrane remodeling. In this study, we describe a mechanism of salt tolerance in *Arabidopsis* involving the modulation of FREE1 levels, which impacts multivesicular body (MVB) trafficking. Specifically, the ESCRT-I (endosomal sorting complex required for transport-I) component FREE1 (FYVE DOMAIN PROTEIN REQUIRED FOR ENDOSOMAL SORTING 1) regulates vacuole fragmentation to enhance salt tolerance. SOS2 phosphorylates FREE1, leading to its degradation and affecting MVB maturation, thereby reducing MVB-vacuole fusion and regulating endomembrane dynamics in response to salt stress. These findings highlight the adaptive role of the plant endomembrane system in coping with salt stress. (Liu et al., *Plant Cell*, 2024. In press).

(二) 研究成果

发表论文: (*Corresponding author, #These authors contributed equally)

Liang X, Li J, Yang Y*, Jiang C* and Guo Y* (2024) Designing salt stress-resilient crops. Current progress and future challenges. *J integr Plant Biol* 66: 303-329.



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研究方向：植物响应干旱胁迫的机理及表观遗传学的研究。

(一) 研究进展

1、在玉米干旱响应中 Ca^{2+} 不依赖的 ZmCPK2 受到 Ca^{2+} 依赖的 ZmCPK17 抑制

钙震荡可以被不同胁迫诱导。钙依赖的蛋白激酶(CDPKs/CPKs)是一类主要的植物钙解码器，参与各种过程，包括干旱响应。有些 CPKs 是钙不依赖的。我们通过筛选过表达的转基因玉米库，发现了一个抗旱性的负调节因子 ZmCPK2。ZmCPK2 不与钙结合，在短时间 ABA 处理时它的活性受到抑制，在长时间处理时则发生动态变化。ZmCPK2 与钙依赖的 ZmCPK17 互作，且被 ZmCPK17 抑制。ZmCPK17 是一个受 ABA 激活的抗旱性正调节因子。ZmCPK17 通过磷酸化 ZmCPK2 的 T60 位点阻止 ZmCPK2 在细胞核的定位。ZmCPK2 与 ZmYAB15 互作，且能磷酸化 ZmYAB15。ZmYAB15 是一个抗旱性的负调节转录因子 (图 1)。这些结果说明干旱诱导的 Ca^{2+} 能够被抑制 ZmCPK2 的 ZmCPK17 所解码，从而提高植物对水分缺乏的适应性 (Hu et al., *J Integr Plant Biol*, 2024)。

Ca^{2+} -Independent ZmCPK2 is Inhibited by Ca^{2+} -Dependent ZmCPK17 During Drought Response in Maize

Calcium oscillations are induced by different stresses. Calcium-dependent protein kinases (CDPKs/CPKs) are one major group of the plant calcium decoders that are involved in various processes including drought response. Some CPKs are calcium-independent. Here, we identified ZmCPK2 as a negative regulator of drought resistance by screening an overexpression transgenic maize pool. We found that ZmCPK2 does not bind calcium, and its activity is mainly inhibited during short term abscisic acid (ABA) treatment, and dynamically changed in prolonged treatment. Interestingly, ZmCPK2 interacts with and is inhibited by calcium-dependent ZmCPK17, a positive regulator of drought resistance, which is activated by ABA. ZmCPK17 could prevent the nuclear localization of ZmCPK2 through phosphorylation of ZmCPK2T60. ZmCPK2 interacts with and phosphorylates and activates ZmYAB15, a negative transcriptional factor for drought resistance. Our results suggest that drought stress induced Ca^{2+} can be decoded directly by ZmCPK17 that inhibits ZmCPK2, thereby promoting plant adaptation to water deficit (Hu et al., *J Integr Plant Biol*, 2024).

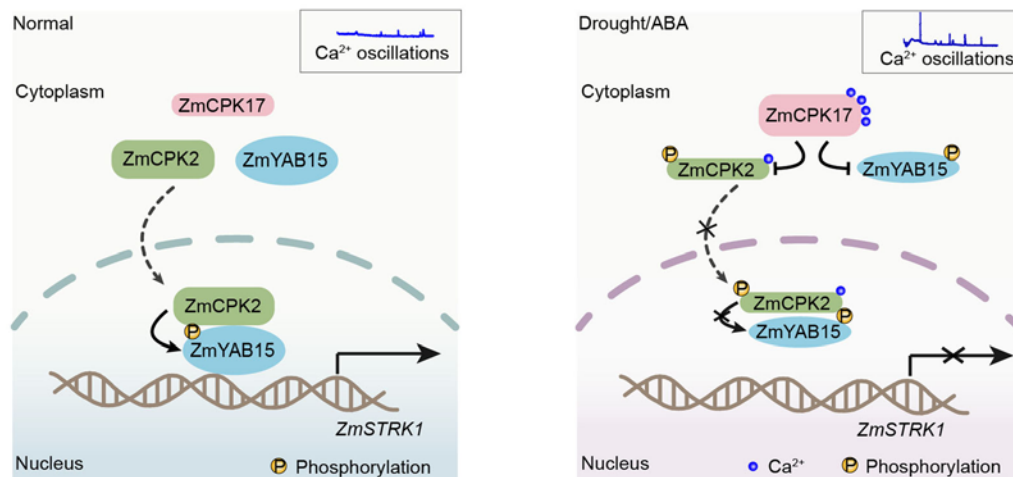


图 1、玉米钙依赖的蛋白激酶 ZmCPK17 在干旱胁迫中与 ZmCPK2 和 ZmYAB15 发挥相反功能。

Figure 1. *Zea mays* calcium-dependent protein kinase 17 (ZmCPK17) plays contrast roles with ZmCPK2 and ZmYAB15 in drought stress.

2、ZmSnRK2.2 磷酸化 ZmAL14 通过解除 *ZmROP8* 的转录抑制调节抗旱性

干旱对作物的生长和产量具有负面影响。发现调节干旱响应基因表达的转录因子对理解干旱应答的转录调控网络至关重要，有助于提高作物抗旱性。我们发现了一个 Alfin-like (AL) 家族基因 *ZmAL14*，负调节玉米抗旱性。过表达 *ZmAL14* 对干旱敏感，而 *ZmAL14* 突变则导致抗旱。ABA 激活的蛋白激酶 ZmSnRK2.2 与 *ZmAL14* 互作且磷酸化 *ZmAL14* 的 T38 位氨基酸。*ZmSnRK2.2* 突变体降低了玉米的耐旱性。脱水诱导的 Rho-like 小 G 蛋白基因 *ZmROP8* 是 *ZmAL14* 的直接靶点，且被 *ZmAL14* 抑制。ZmSnRK2.2 磷酸化 *ZmAL14* 阻止了其与 *ZmROP8* 启动子的结合，解除了 *ZmROP8* 的转录抑制。干旱处理后，过表达 *ZmROP8* 增强了 POD 的酶活，降低了 H_2O_2 的积累。我们的研究表明，*ZmAL14* 是玉米抗旱性的负调节因子，在干旱响应过程中，*ZmAL14* 通过 ABA 信号途径被 ZmSnRK2.2 磷酸化，阻止了它对 *ZmROP8* 转录的抑制 (Wang et al., *J Integr Plant Biol*, 2024)。

Phosphorylation of ZmAL14 by ZmSnRK2.2 Regulates Drought Resistance Through Derepressing *ZmROP8* Expression

Drought stress has negative effects on crop growth and production. Characterization of transcription factors that regulate the expression of drought-responsive genes is critical for understanding the transcriptional regulatory networks in response to drought, which facilitates the improvement of crop drought tolerance. Here, we identified an Alfin-like (AL) family gene *ZmAL14* that negatively regulates drought resistance. Overexpression of *ZmAL14* exhibits susceptibility to drought while mutation of *ZmAL14* enhances drought resistance. An abscisic acid (ABA)-activated protein kinase ZmSnRK2.2 interacts and phosphorylates *ZmAL14* at T38 residue. Knockout of

ZmSnRK2.2 gene decreases drought resistance of maize. A dehydration - induced Rho - like small guanosine triphosphatase gene *ZmROP8* is directly targeted and repressed by ZmAL14. Phosphorylation of ZmAL14 by ZmSnRK2.2 prevents its binding to the *ZmROP8* promoter, thereby releasing the repression of *ZmROP8* transcription. Overexpression of *ZmROP8* stimulates peroxidase activity and reduces hydrogen peroxide accumulation after drought treatment. Collectively, our study indicates that ZmAL14 is a negative regulator of drought resistance, which can be phosphorylated by ZmSnRK2.2 through the ABA signaling pathway, thus preventing its suppression on *ZmROP8* transcription during drought stress response (Wang et al., *J Integr Plant Biol*, 2024).

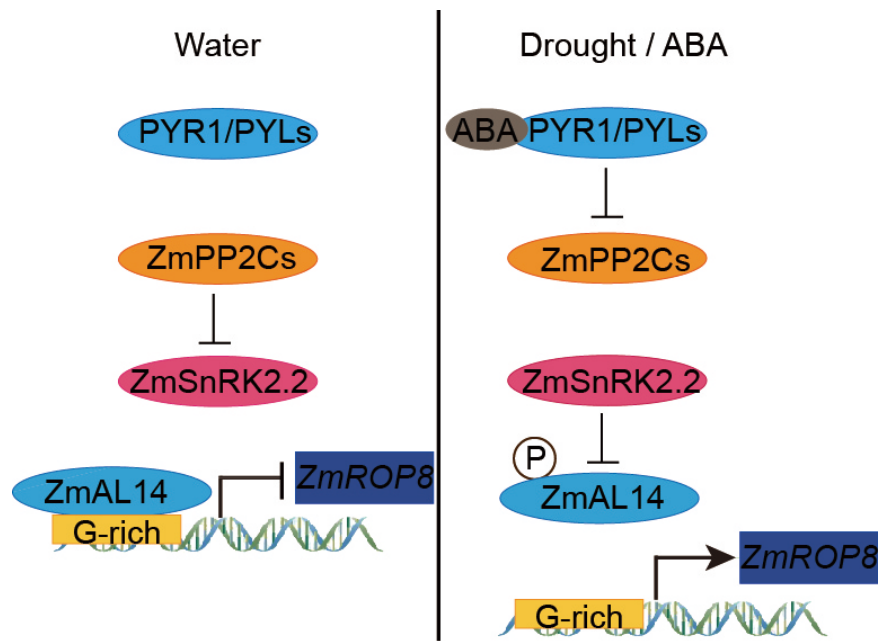


图 2、ZmAL14 负调节玉米干旱响应的模式图。
Figure 2. A proposed model in which ZmAL14 negatively regulates drought response in maize.

(二) 研究成果

发表论文：(*Corresponding author)

1. Hu X, Cheng J, Lu M, Fang T, Zhu Y, Li Z, Wang X, Wang Y, Guo Y, Yang S, Gong Z* (2024) Ca²⁺ - independent ZmCPK2 is inhibited by Ca²⁺ - dependent ZmCPK17 during drought response in maize. *J Integr Plant Biol* 66: 1313-1333.
2. Wang Y, Cheng J, Guo Y, Li Z, Yang S, Wang Y*, Gong Z (2024) Phosphorylation of ZmAL14 by ZmSnRK2.2 regulates drought resistance through derepressing *ZmROP8* expression. *J Integr Plant Biol* 66: 1334-1350.



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(一) 研究进展

1、ECAP-LUG-BEH3 复合体调控小孢子母细胞发生的分子机制研究

拟南芥 (*Arabidopsis thaliana*) 花药的组织特化和形态建成在发育过程中的机制已被广泛研究。然而, 对于减数分裂前的小孢子母细胞发生的调控仍知之甚少, 尤其是孢原细胞如何被特化并进一步分化为具有不同发育命运的两类细胞仍然是未解之谜。SPOROCTELESS (SPL) 是花药发育中的一个关键基因, 在早期阶段被激活并持续表达。在本研究中, 我们发现含 EAR 结构域的衔接蛋白 (EAR motif-containing adaptor protein, ECAP) 通过与 Gro/Tup1 家族的共抑制因子 LEUNIG (LUG) 以及 BES1/BZR1 HOMOLOG3 (BEH3) 转录因子相互作用, 形成一个转录激活复合体, 从而实现对 SPL 基因的表观遗传调控。SPL 调控孢原细胞的特化及后续分化为体细胞层和生殖细胞层的机制, 在小孢子母细胞发生中发挥关键作用。本研究揭示了 ECAP-LUG-BEH3 复合体对 SPL 表达的调控机制, 还发现 ECAP 作为一个重要的转录调节因子, 能够通过与不同蛋白结合, 特异调控不同基因的表达, 从而在植物发育的各个过程中发挥不同的调控作用 (Shi et al., *Plant Cell*, 2024)。

The Adaptor Protein ECAP, the Corepressor LEUNIG, and The Transcription Factor BEH3 Interact and Regulate Microsporocyte Generation in *Arabidopsis*

Histospecification and morphogenesis of anthers during development in *Arabidopsis* (*Arabidopsis thaliana*) are well understood. However, the regulatory mechanism of microsporocyte generation at the pre-meiotic stage remains unclear, especially how archesporial cells are specified and differentiate into 2 cell lineages with distinct developmental fates. SPOROCTELESS (SPL) is a key reproductive gene that is activated during early anther development and remains active. In this study, we demonstrated that the EAR motif-containing adaptor protein (ECAP) interacts with the Gro/Tup1 family corepressor LEUNIG (LUG) and the BES1/BZR1 HOMOLOG3 (BEH3) transcription factor to form a transcription activator complex, epigenetically regulating SPL transcription. SPL participates in microsporocyte generation by modulating the specification of archesporial cells and the archesporial cell-derived differentiation of somatic and reproductive cell layers. This study illustrates the regulation of SPL expression by the ECAP-LUG-BEH3 complex, which is essential for the generation of microsporocytes. Moreover, our findings identified ECAP as

a key transcription regulator that can combine with different partners to regulate gene expression in distinct ways, thereby facilitating diverse processes in various aspects of plant development (Shi et al., *Plant Cell*, 2024).

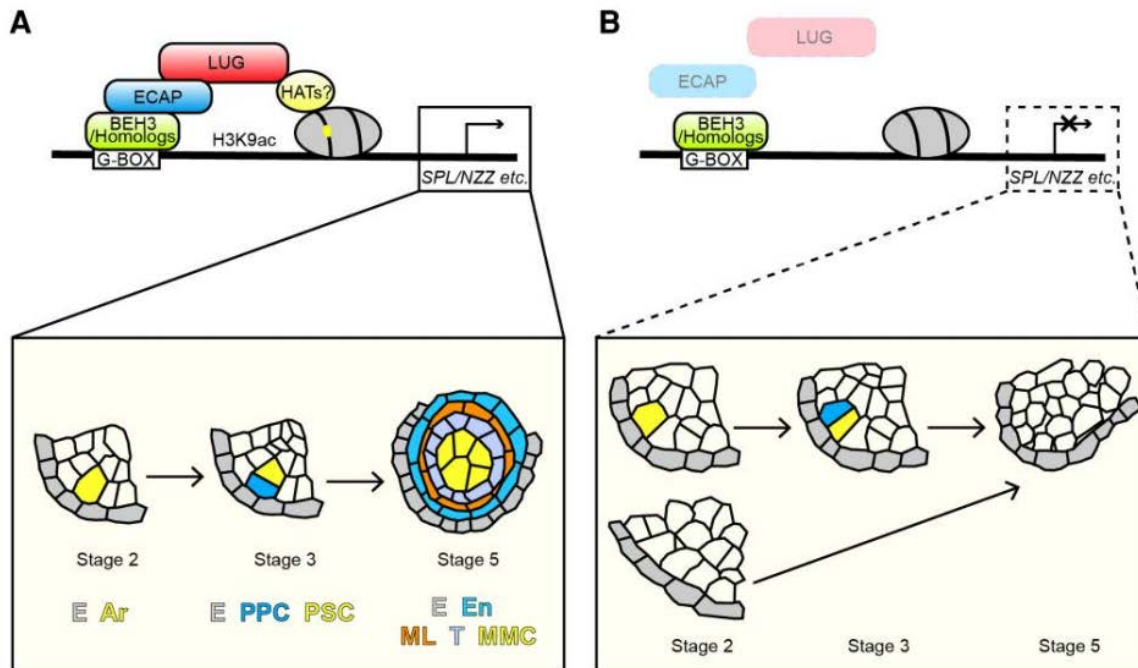


图1、ECAP-LUG-BEH3模块调控拟南芥小孢子母细胞发生的分子机制模型。

Figure 1. A proposed working model for the ECAP-LUG-BEH3 module in regulating microsporocyte generation.

2、拟南芥 LKS4 介导的 SYP121 磷酸化参与光诱导的气孔开放机制研究

通过调节气孔的开闭，植物能够响应不同环境信号控制气体交换、水分散失以及光合作用。在光诱导的气孔开放过程中，围绕气孔的保卫细胞中离子和溶质的跨膜运输导致膨压增加，从而引起细胞膨胀。同时，囊泡被递送到质膜附近并通过胞吐作用补充细胞表面积增大所需的膜组分并维持质膜上适当的离子通道密度。在真核细胞中，可溶性 N-乙基马来酰亚胺敏感因子适配蛋白受体 (SNARE) 通过相应的 Q-和 R-SNARE 的配对，形成核心 SNARE 复合体，介导囊泡与靶膜的融合。植物 Syntaxin of Plants 121 (SYP121) 已被报道参与气孔运动，其作用机制除了能够促进钾离子通道经胞吞回收重新分布到质膜外，还能与离子通道结合以调控后者的通道活性。在本研究中，我们发现受光诱导的胞质类受体激酶 LKS4/SGN1 (low-K⁺ sensitive 4/schengen 1) 可以直接与 SYP121 相互作用，并在 SNARE 基序中的 T270 位点对其进行磷酸化。进一步研究表明，LKS4 依赖的 SYP121 磷酸化促进了 SYP121 与 R-SNARE vesicle-associated membrane protein 722 (VAMP722) 之间的相互作用，从而增强了 SNARE 复合体的组装。我们的研究表明，SNARE 蛋白的磷酸化是植物调控 SNARE 复合体组装和膜融合的重要策略。此外，还揭示了 LKS4/SGN1 通过磷酸化 SYP121，在光诱导的气孔开启中发挥关键作用 (Ding et al., *Curr Biol*, 2024)。

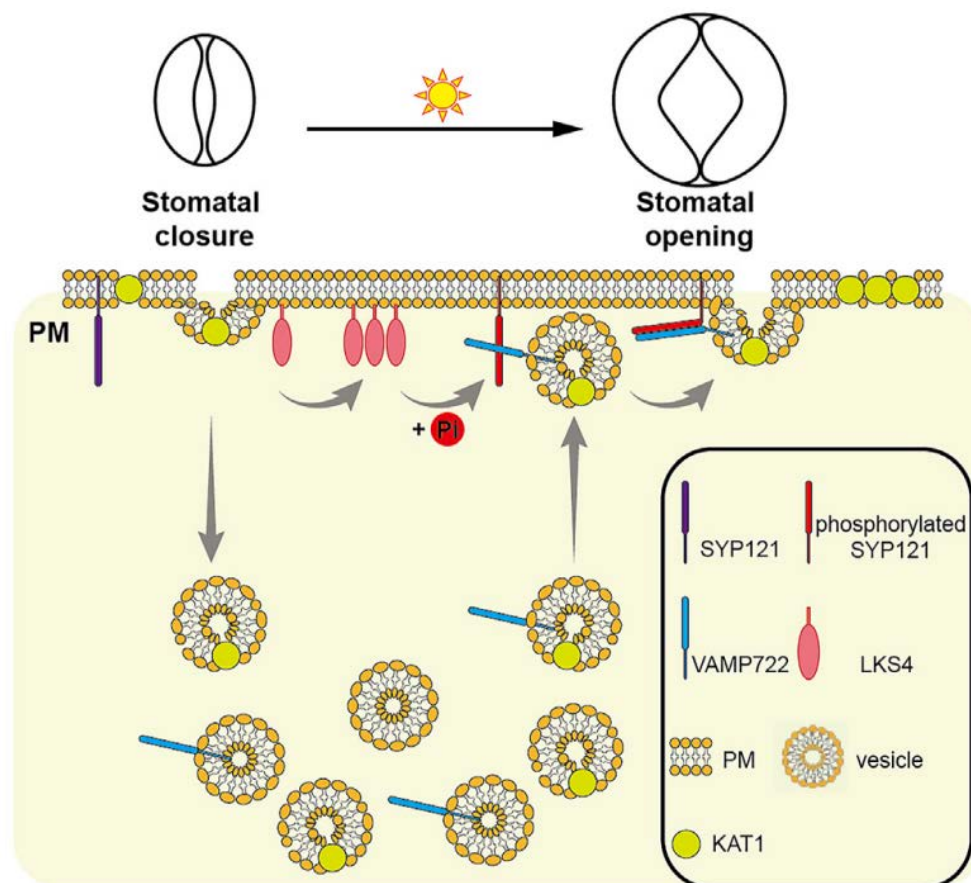


图2、LKS4介导的SYP121磷酸化在调控光诱导气孔开放中的工作模型。

Figure 2. A working model of LKS4-mediated SYP121 phosphorylation in the regulation of light-induced stomatal opening.

LKS4-Mediated SYP121 Phosphorylation Participates in Light-Induced Stomatal Opening in *Arabidopsis*

By modulating stomatal opening and closure, plants control gas exchange, water loss, and photosynthesis in response to various environmental signals. During light-induced stomatal opening, the transport of ions and solutes across the plasma membrane (PM) of the surrounding guard cells results in an increase in turgor pressure, leading to cell swelling. Simultaneously, vesicles for exocytosis are delivered via membrane trafficking to compensate for the enlarged cell surface area and maintain an appropriate ion-channel density in the PM. In eukaryotic cells, soluble N-ethylmaleimide-sensitive factor adaptor protein receptors (SNAREs) mediate membrane fusion between vesicles and target compartments by pairing the cognate glutamine (Q)- and arginine (R)-SNAREs to form a core SNARE complex. Syntaxin of plants 121 (SYP121) is a known Q-SNARE involved in stomatal movement, which not only facilitates the recycling of K^+ channels to the PM but also binds to the channels to regulate their activity. In this study, we found that the expression of a receptor-like cytoplasmic kinase, low- K^+ sensitive 4/schengen 1 (LKS4/SGN1), was induced



by light; it directly interacted with SYP121 and phosphorylated T270 within the SNARE motif. Further investigation revealed that LKS4-dependent phosphorylation of SYP121 facilitated the interaction between SYP121 and R-SNARE vesicle-associated membrane protein 722 (VAMP722), promoting the assembly of the SNARE complex. Our findings demonstrate that the phosphorylation of SNARE proteins is an important strategy adopted by plants to regulate the SNARE complex assembly as well as membrane fusion. Additionally, we discovered the function of LKS4/SGN1 in light-induced stomatal opening via the phosphorylation of SYP121 (Ding et al., *Curr Biol*, 2024).

3、拟南芥微管生长驱动的囊泡运输参与调控气孔运动

基于微管的囊泡运输通常依赖于马达蛋白即驱动蛋白 (kinesin) 和动力蛋白 (dynein), 而关于微管通过聚合生长驱动定向囊泡运输的报道却还没有。在本研究中, 我们发现拟南芥微管正端结合蛋白 END BINDING1b (EB1b) 与 Q-SNARE 蛋白 SYP121 直接相互作用, 参与调控内向 K^+ 通道 KAT1 的运输及其在保卫细胞质膜 (PM) 上的分布。敲除 AtEB1b 及其同源蛋白会导致 KAT1 和 SYP121 在保卫细胞中的分布模式发生变化, 从而延缓光诱导的气孔开放过程。活细胞实时成像显示, 部分带有 SYP121 的囊泡与微管正端的 AtEB1b 共定位, 并随微管的聚合生长一起进行运输, 最终定位于质膜。我们的研究揭示了一种由微管生长驱动的囊泡运输机制, 这一机制参与了保卫细胞质膜上蛋白如离子通道的再分布, 从而调控气孔运动 (Zhong et al., *Nat Commun*, 2024)。

Endomembrane Trafficking Driven by Microtubule Growth Regulates Stomatal Movement in *Arabidopsis*

Microtubule-based vesicle trafficking usually relies upon kinesin and dynein motors and few reports describe microtubule polymerisation driving directional vesicle trafficking. Here we show that *Arabidopsis* END BINDING1b (EB1b), a microtubule plus-end binding protein, directly interacts with SYP121, a SNARE protein that mediates the trafficking of the K^+ channel KAT1 and its distribution to the plasma membrane (PM) in *Arabidopsis* guard cells. Knockout of AtEB1b and its homologous proteins results in a modest but significant change in the distribution of KAT1 and SYP121 in guard cells and consequently delays light-induced stomatal opening. Live-cell imaging reveals that a portion of SYP121-associated endomembrane compartments co-localise with AtEB1b at the growing ends of microtubules, trafficking along with the growth of microtubules for targeting to the PM. Our study reveals a mechanism of vesicle trafficking driven by microtubule growth, which is involved in the redistribution of PM proteins to modulate guard cell movement (Zhong et al., *Nat Commun*, 2024).

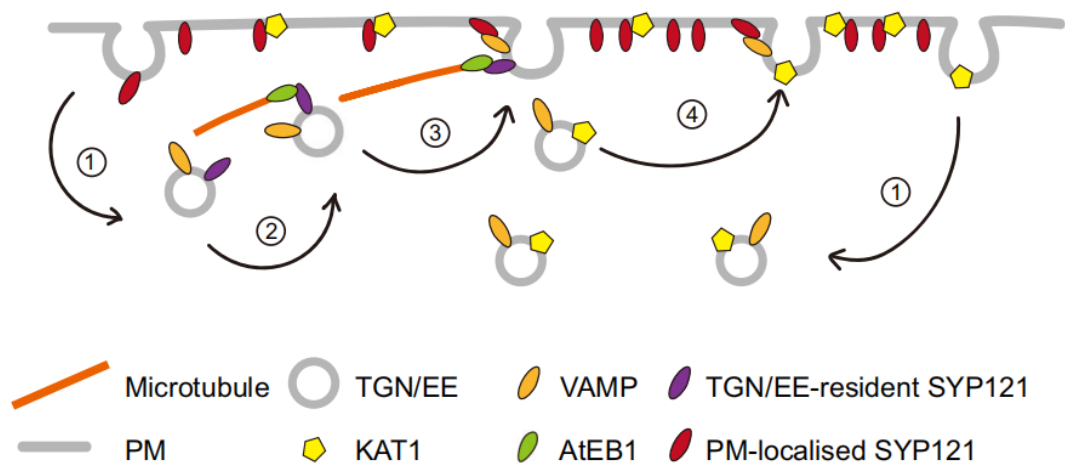


图3、微管聚合生长驱动的囊泡运输调控气孔开放的工作模型。

Figure 3. A working model for the endomembrane trafficking driven by microtubule growth in guard cells during stomata opening.

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

1. Li X[#], Li C^{**}, Shi L, Lv G, Li X, Liu Y, Jia X, Liu J, Chen Y, Zhu L, Fu Y* (2024) Jasmonate signaling pathway confers salt tolerance through a NUCLEAR FACTOR-Y trimeric transcription factor complex in *Arabidopsis*. **Cell Rep** 43: 113825.
2. Shi L[#], Li C[#], Lv G, Li X, Feng W, Bi Y, Wang W, Wang Y, Zhu L, Tang W, Fu Y* (2024) The adaptor protein ECAP, the co-repressor LEUNIG, and the transcription factor BEH3 interact and regulate microsporocyte generation in *Arabidopsis*. **Plant Cell** 36: 2531-2549.
3. Ding X, Wang S, Cui X, Zhong H, Zou H, Zhao P, Guo Z, Chen H, Li C, Zhu L, Li J, Fu Y* (2024) LKS4-mediated SYP121 phosphorylation participates in light-induced stomatal opening in *Arabidopsis*. **Curr Biol** 34: 3102-3115.
4. Zhong H[#], Wang S[#], Huang Y, Cui X, Ding X, Zhu L, Yuan M, Fu Y* (2024) Endomembrane trafficking driven by microtubule growth regulates stomatal movement in *Arabidopsis*. **Nat Commun** 15: 7967.



(三) 研究队伍

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(一) 研究进展

1、玉米果糖 1,6-二磷酸醛缩酶的鉴定与磷酸化调控机制

果糖1,6-二磷酸醛缩酶(FBA)是一种醛缩酶,催化果糖1,6-二磷酸(FBP)可逆地转化为二羟基丙酮磷酸(DHAP)和甘油醛-3-磷酸(G3P),参与卡尔文-本森循环、糖异生和糖酵解的代谢途径,在碳水化合物代谢中发挥重要,同时也作为非酶蛋白参与蛋白质结合、基因转录和信号转导等生物学过程,例如,FBA能够结合一系列伴侣蛋白,调控RNA聚合酶 III导向的转录,介导葡萄糖感应。根据FBAs的催化机制和进化起源可分为I类和II类两个类别。尽管在一些植物中已经鉴定出多个FBA蛋白,但关于玉米(*Zea mays*)中FBA家族的基因、生物学功能和翻译后调控等信息仍十分有限。在本研究中,我们鉴定了玉米中的九个I类FBA (ZmFBA1-9) 和一个II类FBA (ZmFBA10)。磷酸化蛋白质组分析结果显示多个ZmFBA存在磷酸化修饰。进一步研究发现Ser32的磷酸化抑制ZmFBA8对FBP的结合活性和酶活性。ZmFBA8的基因敲除突变体幼苗生长迟缓。这些研究结果表明磷酸化是ZmFBA8功能的一个重要调控机制,为理解FBA的功能和调控机制提供了理论依据 (Zhang et al., *Plant Sci*, 2024)。

Identification of the Fructose 1,6-Bisphosphate Aldolase (FBA) Family Genes in Maize and Analysis of the Phosphorylation Regulation of ZmFBA8

Fructose 1,6-bisphosphate aldolase (FBA) is a class of aldolase that functions as enzyme participating in carbohydrate metabolism of the Calvin-Benson cycle, gluconeogenesis, and glycolysis, and also as non-enzymatic protein involving in protein binding, gene transcription, signal transduction. FBAs have been identified in a few plant species, however, limited information is known regarding FBA family genes, their biological functions and posttranslational regulations in maize (*Zea mays*). In this study, nine class I FBAs (ZmFBA1 to ZmFBA9) and one class II FBA (ZmFBA10) in maize were identified. Phosphoproteomic analysis further revealed that multiple ZmFBAs were phosphorylated. We showed that phosphorylation at Ser32 in ZmFBA8 inhibited its FBP binding and enzyme activity. Loss of ZmFBA8 function reduced the growth of maize seedlings.



于研究蛋白激酶—底物的信号网络具有高分辨率、高精确性等优势，这是传统生化方法无法比拟的。Tandem MOAC 与 AP-BNPAGE 结合不仅能够系统地鉴定激酶的直接底物和非底物邻近(互作)蛋白，还能深入研究内源性底物的分子功能。这些技术为探索蛋白激酶的磷酸化基序和底物提供了高效手段，为研究各类激酶的功能与分子机制提供了新方法。陈艳梅和任东涛受邀联合撰写综述，阐述了 Tandem MOAC 和 AP-BNPAGE 实验流程的优势和在实验应用中的注意事项 (Chen et al., *Trends Plant Sci*, 2024)。

Capturing the Phosphorylation-Linked Protein-Complex Landscape in Plants

Protein phosphorylation and protein interactions are core regulatory systems involved in plant growth and environmental adaptation. Elucidating the intricate isoforms of a protein and its complex-specific phosphosites is critical for understanding intracellular signaling networks, but is technically challenging due to the transient nature of kinase-substrate interactions and the numerous kinases acting in plant cells. Recent improvements in phosphoproteomic and interactomic technologies have boosted kinase research, enabling large-scale studies. Tandem metal oxide affinity chromatography (tandem MOAC) allows global analysis of protein phosphorylation dynamics of key signaling components. Affinity purification by blue native polyacrylamide gel electrophoresis (AP-BNPAGE) allows effective separation of phosphorylation-dependent protein interactions. Tandem MOAC and AP-BNPAGE, coupled with data-independent acquisition-based mass spectrometry (MS) proteomics, can be used to systematically dissect phosphorylation-dependent protein complexes and define the biochemical context of protein kinases (Chen et al., *Trends Plant Sci*, 2024).

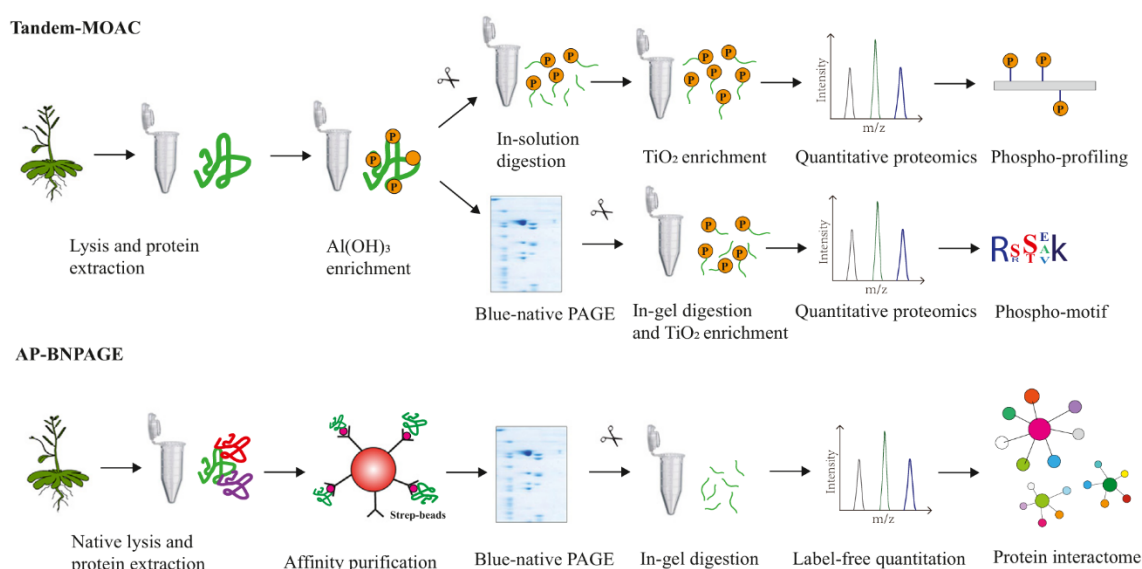


图2、Tandem MOAC和AP-BNPAGE实验流程。

Figure 2. Tandem MOAC and AP-BNPAGE procedures.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Chen Y*, Gu M, Peng J, Li Y, Ren D* (2024) Capturing the phosphorylation-linked protein-complex landscape in plants. *Trends Plant Sci* 29: 823-824.

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课题组

秦峰，教授。国家杰出青年科学基金获得者
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研究方向：玉米抗旱性相关基因克隆与遗传
解析。

(一) 研究进展

ZmMIK2 负调控玉米抵抗盐胁迫和干旱胁迫的分子机制

ZmMIK2 编码一个膜定位的 LRR 型类受体蛋白激酶，是拟南芥 LRR-RK MALE DISCOVERER 1 (MDIS1)- INTERACTING RECEPTOR LIKE KINASE 2 (MIK2)的同源蛋白。该研究发现，相比于野生型植株，*Zmmik2* 突变体株系对于干旱胁迫和盐胁迫处理都表现出抗性增强的表型，而过表达 *ZmMIK2* 的玉米株系则表现出相反的表型，表明 ZmMIK2 负调控玉米对于干旱和盐胁迫的响应。利用酵母双杂交筛选，鉴定了一个编码具有 C2 结构域的蛋白(C2- domain containing PROTEIN 1, ZmC2DP1) 与 ZmMIK2 的胞内域存在相互作用。进一步研究发现，ZmMIK2 的胞内域通过介导 ZmC2DP1 的磷酸化增强其稳定性。而 ZmC2DP1 可能通过与钙离子结合，减弱了干旱或盐胁迫引起的早期胞内 Ca^{2+} 信号，从而负调控玉米对胁迫的响应，推测 ZmMIK2-ZmC2DP1 模块可能在降低玉米植株对环境因子波动的敏感度中发挥作用。本研究揭示了 ZmMIK2-ZmC2DP1 负调控玉米抵抗盐胁迫和干旱胁迫的分子机制，为玉米抗逆性改良育种提供了新的靶点和思路 (Yang et al., *J Genet Genomics* , 2024)。

An LRR-RLK Protein Modulates Drought- And Salt-Stress Responses in Maize

Maize (*Zea mays*), which is a vital source of food, feed, and energy feedstock globally, has significant potential for higher yields. However, environmental stress conditions, including drought and salt stress, severely restrict maize plant growth and development, leading to great yield losses. Leucine-rich repeat receptor-like kinases (LRR-RLKs) function in biotic and abiotic stress responses in the model plant *Arabidopsis* (*Arabidopsis thaliana*), but their roles in abiotic stress responses in maize are not entirely understood. In this study, we determine that the LRR-RLK ZmMIK2, a homolog of the *Arabidopsis* LRR-RK MALE DISCOVERER 1 (MDIS1)- INTERACTING RECEPTOR LIKE KINASE 2 (MIK2), functions in resistance to both drought and salt stress in maize. *Zmmik2* plants exhibit enhanced resistance to both stresses, whereas overexpressing *ZmMIK2* confers the opposite phenotypes. Furthermore, we identify C2-DOMAIN-CONTAINING PROTEIN 1 (ZmC2DP1), which interacts with the intracellular region of ZmMIK2. Notably, that region of ZmMIK2 mediates the phosphorylation of ZmC2DP1, likely by increasing its



stability. Both *ZmMIK2* and *ZmC2DP1* are mainly expressed in roots. As with *ZmMIK2*, knockout of *ZmC2DP1* enhanced resistance to both drought and salt stress. We conclude that *ZmMIK2*–*ZmC2DP1* act as a negative regulatory module in maize drought- and salt-stress responses (Yang et al., *J Genet Genomics*, 2024).

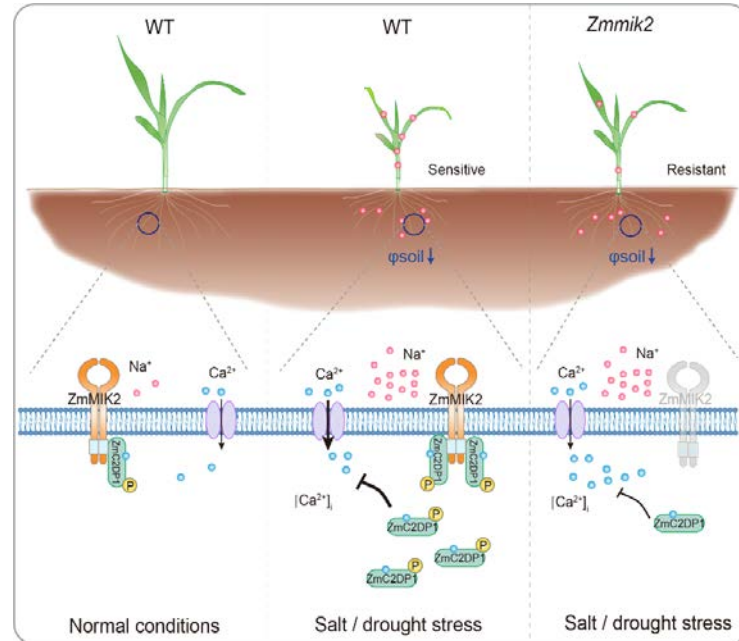


图1、ZmMIK2-ZmC2DP1负向调控玉米对非生物胁迫的响应的工作模型。

Figure 1. A proposed working model for the role of *ZmMIK2*–*ZmC2DP1* in negatively regulating the response of maize to abiotic stress.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Yang Z#, Wang C#, Zhu T, He J, Wang Y, Yang S, Liu Y, Zhao B, Zhu C, Ye S, Chen L, Liu S, Qin F* (2024) An LRR-RLK protein modulates drought- and salt-stress responses in maize. *J Genet Genomics* 13:S1673-8527(24)00293-5. DOI: 10.1016/j.jgg.2024.10.016.
2. Yang Z, Li G, Zhang Y, Li F, Zhou T, Ye J, Wang X, Zhang X, Sun Z, Tao X, Wu M, Wu J, Li Y (2024) Crop antiviral defense: Past and future perspective. *Sci China Life Sci* DOI: 10.1007/s11427-024-2680-3.

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毛同林，教授。国家杰出青年科学基金获得者(2016)。

研究方向：细胞骨架参与植物细胞响应环境信号的分子机制。

(一) 研究进展

1、PUB25-PBL4 元件通过微管骨架调控气孔运动的细胞学机制

气孔的关闭与张开对于植物体内的水分平衡至关重要，影响着光合作用和蒸腾作用等诸多重要的生理学过程。光照是调节气孔运动最主要的环境因素之一。气孔在光下张开，黑暗下关闭。微管是植物细胞骨架的重要组成部分，微管骨架的组织 and 动态变化对于气孔运动至关重要。我们课题组发现一个胞质类受体激酶 *PBL4* 的功能缺失突变体在暗转光条件下气孔张开速度显著滞后于野生型，且 *PBL4* 与微管骨架共定位，是一个微管结合蛋白，通过稳定微管骨架正调控气孔在光下的张开过程。进一步的研究发现 *PBL4* 的蛋白水平受光调控，暗下发生降解而光下稳定。E3 泛素连接酶 *PUB25* 与 *PBL4* 互作，*PBL4* 在暗下被 *PUB25* 泛素化修饰并降解；在光下 *PUB25* 转录水平下调，*PBL4* 蛋白更加稳定，从而促进微管聚合正调控光诱导的气孔张开过程。该项研究发现了微管骨架参与光暗诱导气孔运动的一个重要机制，丰富了微管参与气孔运动的调控网络，为未来分子育种和提高植物环境适应性提供了重要的信息。

Mechanisms of E3 Ubiquitin Ligase PUB25 in Regulating the Microtubule-Associated Protein PBL4 During Light-Induced Stomatal Opening

The opening and closure of stomata are pivotal for plants and have profound implications for essential physiological processes. Light is recognized as a primary environmental signal that orchestrates stomatal movements. Microtubules play a critical role in mediating light-induced stomatal movement. In this study, we identified a mutant of the receptor-like cytoplasmic kinase, *PBL4*, which exhibits a significantly attenuated response in stomatal opening during transitions from dark to light. Subsequent analyses of *PBL4* revealed that it functions as a microtubule-associated protein, positively regulating light-induced stomatal opening through the stabilization of the microtubule cytoskeleton. The *PBL4* protein is stable in light but degrades in the dark. Further research demonstrated that the E3 ubiquitin ligase *PUB25* interacts with *PBL4* both in vivo and in vitro. During dark-induced stomatal closure, the *pub25* mutant showed a delayed closure rate compared to the wild-type control. Importantly, *PBL4* undergoes ubiquitination and subsequent degradation by *PUB25* under dark conditions. In contrast, exposure to light leads to the

downregulation of *PUB25* transcription, enhancing the stability of the PBL4 protein. This stabilization promotes microtubule polymerization, facilitating the positive regulation of stomatal opening in response to light. This study reveals an important mechanism by which the microtubule cytoskeleton participates in light and dark-induced stomatal movements, enriching the regulatory network of microtubule involvement in stomatal dynamics and providing valuable insights for future molecular breeding aimed at enhancing plant adaptability.

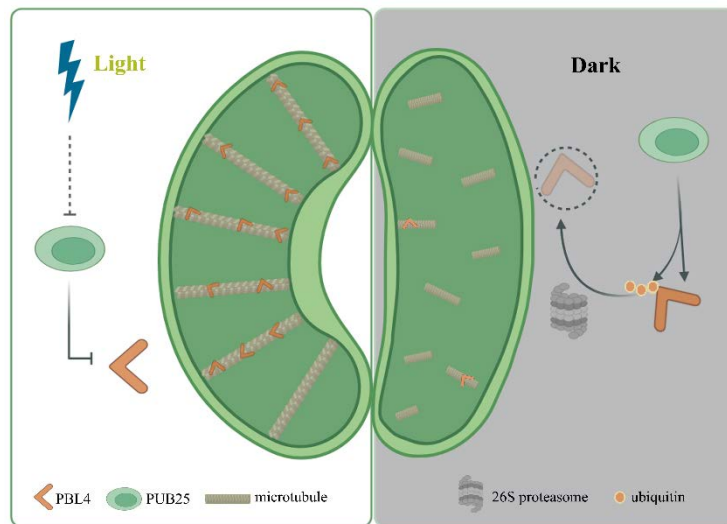


图1、PUB25-PBL4参与光暗诱导气孔运动的假设模型。

Figure 1. Model for PUB25-PBL4's involvement in the regulation of light-induced stomatal movement.

2、微管结合蛋白 **SPR1** 正调控饥饿条件下自噬过程的机制研究

自噬是真核生物中一类保守的蛋白降解途径，对于植物的生长发育及逆境响应至关重要。自噬体的形成及成熟过程依赖于多种核心复合体，其中磷脂酰肌醇3-激酶复合体(PI3K)，包括催化亚基VPS34以及ATG6、ATG14等组分，调控了自噬体的成核过程。在哺乳动物中存在多种调控因子通过调控ATG6来影响PI3K复合体，进而影响自噬过程。目前，在植物中通过调控PI3K复合体影响自噬的具体机制仍不清楚。本研究发现拟南芥中ATG6与微管结合蛋白SPR1存在相互作用。在饥饿条件下，突变体*spr1-6*的表型较野生型更加敏感。细胞学及生化实验进一步验证了SPR1正调控饥饿诱导条件下的自噬过程。在饥饿条件下，SPR1由彗星扫尾定位转化为更多的内质网定位，通过促进ATG6与ATG14的互作来调控PI3K复合体的组装，正调控自噬过程。进一步筛选到自噬途径重要的上游激活因子KIN10能够磷酸化SPR1，持续磷酸化状态的SPR1主要呈现内质网的定位并能够促进ATG6与ATG14的互作。饥饿诱导条件下，磷酸化状态的SPR1从微管上解离下来，更多的结合在内质网上，促进ATG6与ATG14的互作，从而促进PI3K复合体的组装，正调控自噬过程。该研究为探究植物在胁迫环境下调控细胞自噬的具体机制提供了一个新的角度，为微管骨架和微管结合蛋白的功能研究提供了新的信息。



Microtubule-Associated Protein SPR1 Enhances Autophagosome Formation during Carbon Starvation in *Arabidopsis*

Autophagy is a conserved protein degradation pathway in eukaryotes that is essential for plant growth, development, and response to stress. The formation and maturation of autophagosomes rely on various core complexes, with the phosphatidylinositol 3-kinase (PI3K) complex playing a key role in the nucleation process of autophagosomes. This complex includes the catalytic subunit VPS34, along with components such as ATG6 and ATG14. In mammals, several regulatory factors influence the PI3K complex by modulating ATG6, thus affecting the autophagy process. However, the specific mechanisms by which the PI3K complex regulates autophagy in plants are still unclear. This study discovered that ATG6 interacts with the microtubule-binding protein SPR1 in *Arabidopsis*. Under starvation conditions, the *spr1-6* mutant exhibited heightened sensitivity compared to the wild type. Cytological and biochemical experiments further confirmed that SPR1 positively regulates autophagy under starvation-induced conditions. The findings indicated that, during starvation, SPR1 transitions from a cometary tail localization to a more endoplasmic reticulum localization, facilitating the assembly of the PI3K complex by enhancing the interaction between ATG6 and ATG14, thereby promoting the autophagy process. Additionally, this study identified KIN10, a crucial upstream activator of autophagy, as a kinase that phosphorylates SPR1. The continuously phosphorylated SPR1 predominantly localizes to the endoplasmic reticulum and promotes the interaction between ATG6 and ATG14. Under starvation conditions, phosphorylated SPR1 dissociates from microtubules and associates more with the endoplasmic reticulum, further facilitating the assembly of the PI3K complex and positively regulating autophagy. This research provides new insights into the mechanisms by which plants regulate cellular autophagy in response to environmental stress and enhances our understanding functions of microtubule and microtubule-binding proteins.

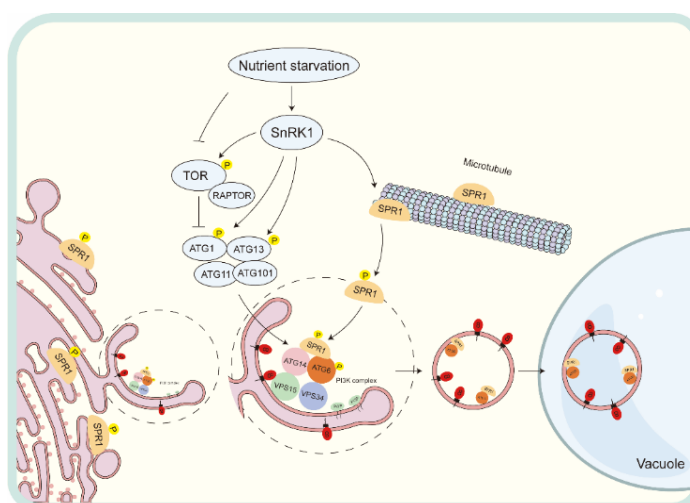


图 2、微管结合蛋白 SPR1 正调控饥饿条件下自噬过程的工作模式图。

Figure 2. Working model: SPR1 promotes autophagosome formation during carbon starvation in *Arabidopsis*.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Qiu T, Su Y, Guo N, Zhang X, Jia P, Mao T, Wang X* (2024) MYB52 negatively regulates ADF9-mediated actin filament bundling in *Arabidopsis* pavement cell morphogenesis. **J Integr Plant Biol** 66: 2379-2394.
2. Xie W, Zhao Y, Deng X, Chen R, Qiang Z, García-Caparrós P, Mao T, Qin T* (2024) GLABRA3-mediated trichome branching requires transcriptional repression of MICROTUBULE-DESTABILIZING PROTEIN25. **Plant Physiol** DOI: 10.1093/plphys/kiae563.

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研究方向：农业生物信息学、功能基因组学和系统生物学研究。

(一) 研究进展

拟南芥核纤层类似蛋白 **KAKU4** 影响染色质状态与调控基因表达的分子机制研究

我们整合和挖掘了已发表文章和公共平台上的蛋白质组学数据，构建了以拟南芥核纤层类似蛋白为核心节点的蛋白-蛋白关联网络，对网络节点的功能分析提示了**KAKU4**可能与组蛋白修饰和染色质状态转变相关。蛋白质印迹分析结果表明**KAKU4**基因功能缺失影响了表观遗传标记H3K27me3和H3K9me2的水平。进一步通过染色质免疫共沉淀高通量测序(ChIP-seq)实验，对生长4周**kaku4-2**突变体和WT的莲座叶进行了H3K4me3, H3K27me3和H3K9me2的表观基因组学分析。结果表明，**KAKU4**基因功能缺失对H3K27me3的影响最大，其次是H3K9me2，对H3K4me3的影响较小。染色质状态分析结果表明**KAKU4**可以微调染色质状态，且在特定的植物核纤层关联区域(PLAD)上，可能存在两种抑制性表观遗传标记H3K9me2和H3K27me3之间的转变。表观基因组和转录组数据的联合分析表明，拟南芥**KAKU4**基因功能缺失显著影响H3K27me3的沉积，进而影响一些关键基因的转录水平。功能富集分析表明，这些基因参与了包括氧化应激、程序性细胞死亡、激素信号转导途径等一系列生物学过程。通过对拟南芥生长过程中叶片相关表型进行观察，发现**kaku4-2**突变体以及**KAKU4** CRISPR/Cas9类型突变体**kaku4-03**, **kaku4-04**和**kaku4-05**都有叶片早衰、叶绿素含量降低的现象。**kaku4-2**突变体中激素水平升高，尤其是水杨酸(SA)、茉莉酸(JA)和脱落酸(ABA)。这些结果表明**KAKU4**可能通过影响H3K27me3的沉积来调控多种激素信号和叶片衰老 (Cao et al., *BMC Biology*, 2024; *BMC Plant Biology*, 2024)。

Nuclear Lamina Component KAKU4 Regulates Chromatin States and Transcriptional Regulation in the *Arabidopsis* Genome

KAKU4 is a putative nuclear lamina component protein and associated with chromatin or epigenetic modifiers. We conducted ChIP-seq technology to generate epigenomic profiles of H3K4me3, H3K27me3 and H3K9me2 in *Arabidopsis* leaves for the mutant (*kaku4-2*) and wild-type (WT) plants. The results showed that knockdown of **KAKU4** has the strongest effect on H3K27me3,



followed by H3K9me2, and the least effect on H3K4me3, leading to significant change of chromatin states in *Arabidopsis* genome. KAKU4 may affect the switch between active and repressive chromatin states, especially knockdown of *KAKU4* caused the transition between H3K9me2 and H3K27me3 in some specific PLAD regions. The combination analysis of epigenomic and transcriptomic data between *kaku4-2* mutant and WT suggested that KAKU4 may regulate some key biological processes, especially programmed cell death and hormone signaling pathways. In addition, there are functional crosstalks between KAKU4 and its associated proteins (CRWN1/4, PNET2, GBPL3). Further experiments validated that mutation of *KAKU4* resulted in significantly accelerated leaf senescence and elevated levels of H₂O₂, as well as some hormones. In summary, our results demonstrated the essential roles of KAKU4 in fine-tuning chromatin states and gene expression, regulating diverse biological processes in *Arabidopsis* (Cao et al., *BMC Biology*, 2024; *BMC Plant Biology*, 2024).

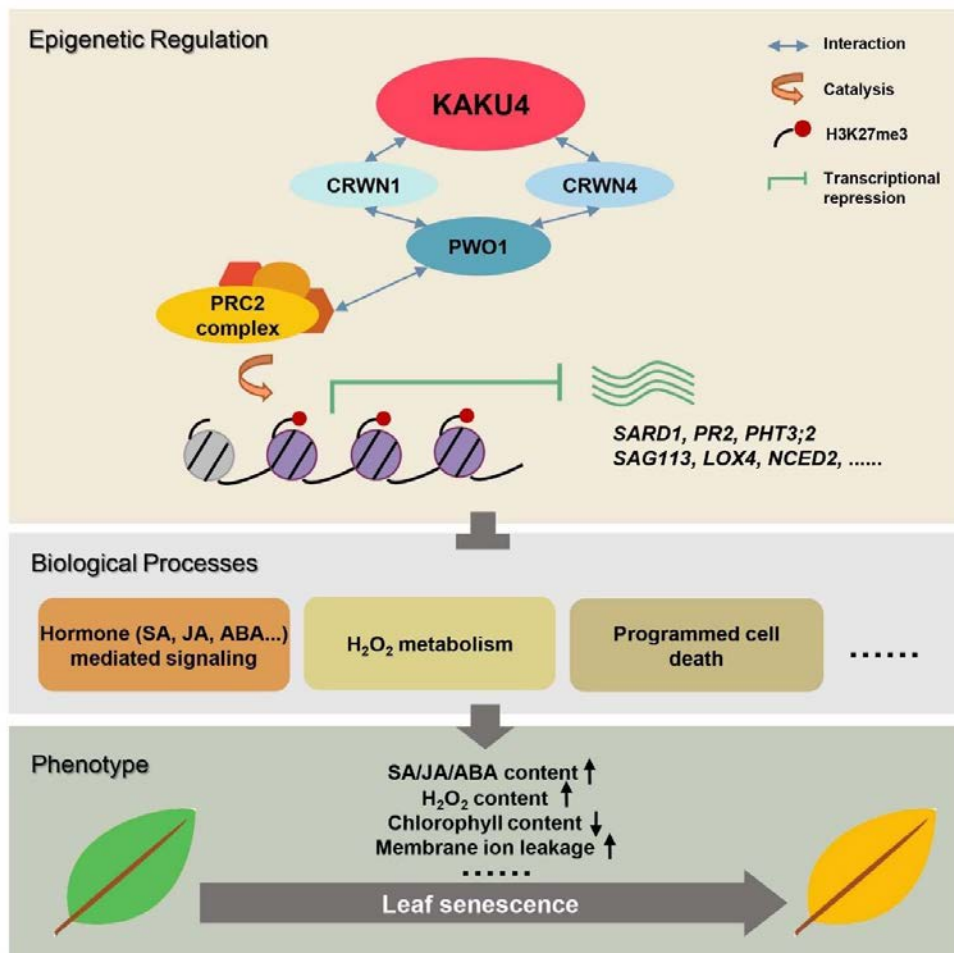


图1、KAKU4 影响染色质状态和基因表达，以及叶片衰老的机制模型。

Figure 1. Model for KAKU4 in fine-tuning chromatin states and gene expression, further affecting leaf senescence.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Cao Y[#], Yan H[#], Sheng M[#], Liu Y, Yu X, Li Z, Xu W, Su Z (2024) Nuclear lamina component KAKU4 regulates chromatin states and transcriptional regulation in the *Arabidopsis* genome. **BMC Biol** 22:80.
2. Cao Y[#], Yan H[#], Sheng M[#], Liu Y, Yu X, Li Z, Xu W, Su Z (2024) KAKU4 regulates leaf senescence through modulation of H3K27me3 deposition in the *Arabidopsis* genome. **BMC Plant Biol** 24:177.

(三) 研究队伍

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(一) 研究进展

1、ABA 诱导 NO 合成调控气孔关闭和干旱胁迫应答的分子机制

脱落酸(Abscissic acid, ABA)诱导的一氧化氮(nitric oxide, NO)积累是触发气孔关闭的必要条件。但 ABA 诱导 NO 合成的分子机制仍不清楚。本研究利用病毒诱导的基因沉默(Virus-induced gene silencing, VIGS)技术干扰 ABA 信号途径中编码关键组分的基因表达，发现沉默开放气孔 1 蛋白激酶的基因 *GhOST1* 可显著抑制 ABA 诱导的保卫细胞中 NO 的富集。为进一步探究 *GhOST1* 在 ABA 诱导的 NO 合成中的作用，我们构建了过表达 *GhOST1* 的棉花植株。当过表达 *GhOST1*，ABA 可诱导更多的 NO 在保卫细胞中合成且植株表现出更强的耐旱能力。为揭示 *GhOST1* 调控 NO 合成的分子机制，我们通过酵母双杂交文库的筛选，获得了 NO 合成前体 L-精氨酸生物合成中的关键限速酶 N-乙酰谷氨酸激酶(N-acetylglutamate kinase, *GhNAGK*)。体外磷酸化和 LC-MS 分析结果表明，*GhOST1* 可以磷酸化 *GhNAGK* 的 Ser60, Ser87, Ser334 和 Thr163/Thr167 位点，进而影响 *GhNAGK* 激酶活性。VIGS-*GhNAGK* 棉花植株的气孔关闭对 ABA 不敏感，而过表达 *GhNAGK* 则增加了 ABA 诱导的保卫细胞中 NO 的积累，增强了植株的耐旱性。此外，外源 L-精氨酸和 NO 供体 SNP 处理可恢复 VIGS-*GhOST1* 或-*GhNAGK* 植株气孔对 ABA 不敏感表型，并显著提高叶片相对含水量，增强棉花耐旱性。同时 NO 合成抑制剂 L-NAME 可显著抑制 ABA 诱导的 NO 的富集，表明 ABA 诱导的 NO 在保卫细胞中富集主要经 NOS-like 途径实现。ABA 与 NO 处理的 S-亚硝化蛋白质组学关联分析发现，两者可通过共同调控参与苹果酸代谢关键酶的 S-亚硝化触发保卫细胞 Cl⁻离子外排介导气孔关闭。上述结果明确了 *GhOST1* 磷酸化调控 NOS-like 途径实现 ABA 诱导保卫细胞中 NO 合成和植株耐旱的分子机制，解析了 NO 和 ABA 调控气孔关闭应答干旱胁迫的亚硝基化调控靶点，为棉花抗逆调控提供了理论依据 (图 1)。



Molecular Mechanism of ABA-Induced NO Synthesis in Regulating Stomatal Closure and Drought Stress Response

The accumulation of nitric oxide (NO) induced by abscisic acid (ABA) is essential for triggering stomatal closure. However, the underlying molecular mechanism remains unclear. In this study, we used virus-induced gene silencing (VIGS) technology to interfere with the gene expression encoding key components in the ABA signaling pathway and found that silencing *GhOST1*, which encodes open stomata 1 protein kinase, significantly inhibited the ABA-induced accumulation of NO in guard cells. To further explore the role of GhOST1 in ABA-induced NO synthesis, we generated cotton plants overexpressing *GhOST1* and found that OE-*GhOST1* plants exhibited more ABA-induced NO synthesis in guard cells and the plants showed stronger drought tolerance. To reveal the molecular mechanism by which GhOST1 regulates NO synthesis, we screened a yeast two-hybrid library and identified N-acetylglutamate kinase (GhNAGK), a key rate-limiting enzyme in the biosynthesis of L-arginine, the precursor of NO. Results from *in vitro* phosphorylation and LC-MS analysis indicated that GhOST1 phosphorylates GhNAGK at Ser60, Ser87, Ser334, and Thr163/Thr167 sites, thereby affecting GhNAGK kinase activity. VIGS-*GhNAGK* cotton plants showed insensitive stomatal closure in response to ABA, while overexpressing *GhNAGK* increased the ABA-induced accumulation of NO in guard cells and enhanced drought tolerance. Furthermore, exogenous L-arginine and the NO donor SNP treatments restored the ABA-insensitive stomatal phenotype of VIGS-*GhOST1* or -*GhNAGK* plants, significantly increased leaf relative water content, and enhanced drought tolerance in cotton. Consistently, the NO synthesis inhibitor L-NAME significantly inhibited the ABA-induced accumulation of NO, suggesting that ABA-induced NO enrichment in guard cells primarily through a NOS-like pathway. Correlation analysis of S-nitrosylated proteomics between ABA and NO treatments revealed that both could trigger guard cell Cl⁻ ion efflux-mediated stomatal closure by jointly regulating the S-nitrosylation of key enzymes involved in malate metabolism. Together, we elucidate the molecular mechanism by which GhOST1 phosphorylates and regulates the NOS-like pathway to modulate ABA-induced NO synthesis in guard cells and identify nitrosylation regulatory targets for NO and ABA in regulating stomatal closure, providing a new insight into the cross-regulation of stomatal closing, as well as plant drought tolerance, by ABA and NO signaling (Figure 1).

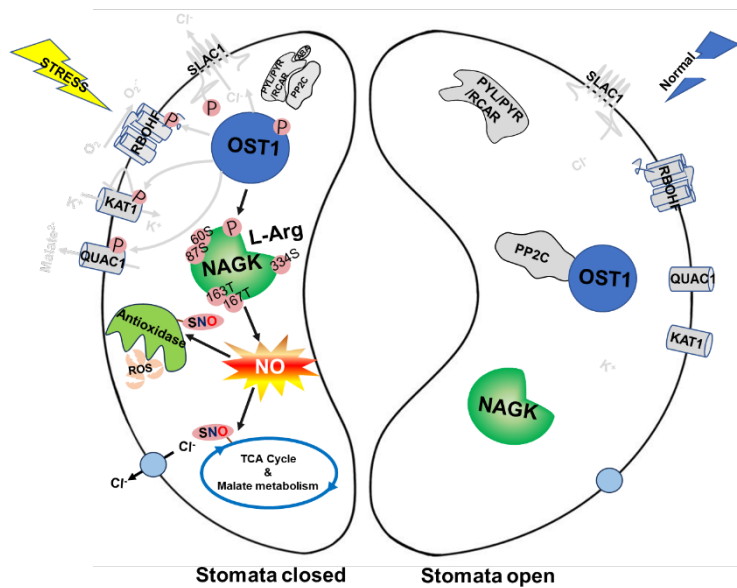


图 1、ABA 诱导 NO 合成调控棉花气孔关闭和干旱胁迫应答的模型。

Figure 1. A proposed model for ABA-induced NO synthesis in regulating stomatal closure and drought stress response in cotton.

2、乙烯抑制盐胁迫下质膜 H⁺-ATPase 降低玉米根系 Na⁺外排打破 Na⁺/H⁺稳态

乙烯在调节植物生长和逆境响应过程中发挥着至关重要的作用。玉米作为中度盐敏感作物，全球范围内的玉米生产受土壤盐害的限制。然而，目前尚不清楚乙烯如何调节 Na⁺/H⁺稳态影响盐胁迫下的玉米生长。前期研究发现，盐胁迫诱导了玉米根系乙烯合成基因的表达并提高了乙烯释放速率。其中，乙烯合成途径关键基因 *ZmACO2* 受盐诱导的表达倍数最高。*ZmACO2* 编码乙烯生物合成酶 1-氨基环丙烷-1-羧酸氧化酶 2，在玉米中将 ACC 转化成乙烯。团队利用 *ZmACO2* 过表达和 CRISPR 敲除材料对盐胁迫的响应，研究乙烯在盐胁迫下调节 Na⁺/H⁺稳态的作用。通过对材料进行盐表型分析，发现 *ZmACO2* 敲除材料盐胁迫下的生长抑制率低于野生型材料，具有耐盐表型，并在盐胁迫下呈现较低的乙烯释放速率和钠钾比。但其 *ZmSOS1* 和 *ZmHKT1* 表达较高，这增加了玉米根系 Na⁺外排，并减少了 Na⁺从根向茎的转运，最终使其根和茎中 Na⁺荧光强度也低于野生型。而玉米根尖离子流速结果表明，*ZmACO2* 敲除材料在盐胁迫下具备较高的 Na⁺外排速率，且原钒酸钠和阿米洛利对其的抑制效率及 *SOS1* 活性均低于野生型，说明乙烯介导玉米根尖 Na⁺外排过程与 *SOS1* 和质膜 H⁺-ATP 酶相关。而 *ZmACO2* 敲除材料质膜 H⁺-ATPase 活性和根尖 H⁺外排速率在盐胁迫下均高于野生型，且 *ZmACO2* 过表达材料与之呈现相反的盐敏感表型，表明乙烯通过抑制质膜 H⁺-ATPase 活性，减少了盐胁迫下玉米根尖 *SOS1* 排 Na⁺所需的质子驱动力。综合各项盐生理及形态指标进行偏最小二乘路径建模，发现盐胁迫下乙烯与 *SOS1*、质膜 H⁺-ATPase 和 *ZmHKT1* 成显著负相关，与玉米植株 Na⁺积累呈显著正相关；质膜 H⁺-ATPase 与 *SOS1* 呈正相关，*SOS1* 对 Na⁺积累有较强的负相关关系，而 Na⁺积累与植物生长呈显著负相关。综上所述，盐诱导的乙烯抑制了质膜 H⁺-



ATPase 酶和 SOS1 活性，破坏 Na^+/H^+ 稳态，从而减少了玉米根系 Na^+ 外排，这为提高盐胁迫下玉米的生产性能提供了可行的策略 (图 2)。

Ethylene Inhibited PM H^+ -ATPase to Decrease Root Na^+ Efflux in Maize to Break Na^+/H^+ Homeostasis under Salt Stress

Ethylene plays indispensable roles in regulating plant growth and stress responses. Maize (*Zea mays* L.) is classified as a moderately salt-sensitive plant, and soil salinity restricts its production worldwide. However, it remains unclear how ethylene regulates Na^+/H^+ homeostasis to mediate maize growth under salt stress. The *ZmACO2* encoding ethylene biosynthesis enzyme 1-aminocyclopropane-1-carboxylate oxidase2 was induced by salt stress, and *ZmACO2* overexpressing (*ACO2-OE*) and mutant (*aco2-cr*) plants were used to investigate the role of ethylene in regulating Na^+/H^+ homeostasis in maize under salt stress. The *aco2-cr* mutants had lower Na^+ accumulation and Na^+/K^+ ratios than the wild-type and *ACO2-OE* plants under salt stress, but they expressed higher *ZmSOS1* and *ZmHKT1*, which increased the root net Na^+ efflux and decreased the Na^+ transport from the root to the shoot. Compared to the other plants, *aco2-cr* mutants showed higher expression of *ZmMHA2* and PM H^+ -ATPase activities, which promoted the net root net H^+ efflux to provide more H^+ proton gradient for salt-overly sensitive 1 (*SOS1*). Inhibition efficiencies of Na^+ efflux and H^+ influx by sodium orthovanadate were lower in *aco2-cr* mutants than in *ACO2-OE* and wild-type plants under salt stress; however, *ACO2-OE* plants showed a salt-sensitive phenotype. To further evaluate the complex causative relationships among ethylene, PM H^+ -ATPase, *SOS1*, *ZmHKT1*, Na^+ accumulation, and plant growth and the complex causative relationships among physiological and morphological data, partial least squares path modeling (PLS-PM) was used to develop a consensus model. Ethylene had a strong negative correlation with PM H^+ -ATPase, *SOS1*, and *ZmHKT1* but had a positive correlation with Na^+ accumulation. PM H^+ -ATPase positively correlated with *SOS1*. *SOS1* had strong negative effects on Na^+ accumulation, and Na^+ accumulation was negatively correlated with plant growth. Overall, these findings showed that salt-induced ethylene treatment inhibited PM H^+ -ATPase and *SOS1* from disrupting Na^+/H^+ homeostasis, thereby decreasing Na^+ efflux in maize roots, which provided a feasible strategy for improving maize performance in saline environments (Figure 2).

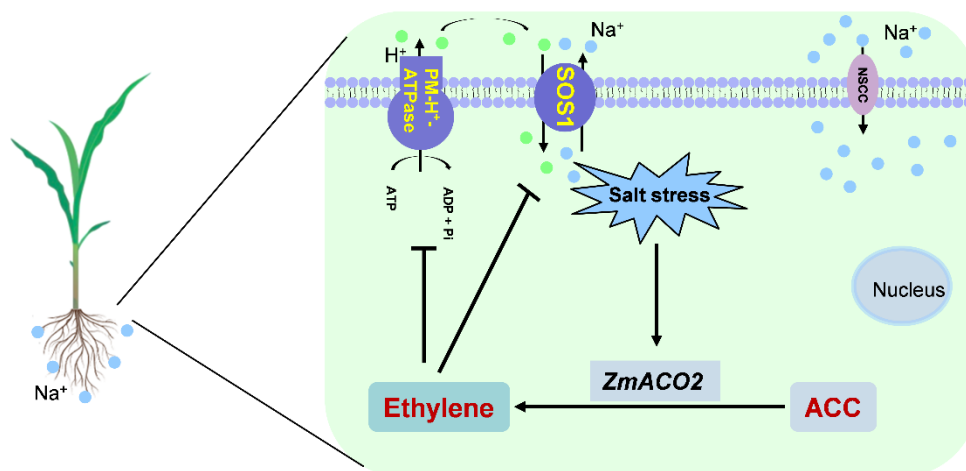


图2、盐胁迫下乙烯通过调控质膜H⁺-ATP酶介导玉米根系Na⁺外排机制的模式图。

Figure 2. Suggested model for how ethylene regulated PM H⁺-ATPases to mediate root Na⁺ efflux under salt stress in maize seedlings.

3、GhMYB4-GhTOPP6a-GhERF9 模块抑制乙烯合成调控棉花的耐盐性

蛋白磷酸酶 1(PP1)是真核生物中一个重要的蛋白磷酸酶家族。随着基因组学的蓬勃发展,越来越多的蛋白磷酸酶在植物中被发现和研究。然而,PP1 在植物抵御非生物胁迫中的作用却鲜有报道。本研究利用病毒诱导的基因沉默(VIGS)检测方法筛选了棉花(*Gossypium hirsutum* L.)cDNA 文库,发现 PP1 家族中的一种蛋白磷酸酶 GhTOPP6a 能正向调节棉花的耐盐性。OE-*GhTOPP6a* 棉花植株表现出耐盐性;而 CRI-*GhTOPP6a* 棉花植株则表现出对盐的敏感性。此外,GhTOPP6a 与乙烯响应因子 GhERF9 相互作用并调控 GhERF9 T81 位点的去磷酸化,从而负向调节 ACC 氧化酶 GhACO3 启动子的转录激活活性。该研究还明确了 GhACO3 的转录水平与乙烯释放有关,对棉花的耐盐性有负向调节作用。外源叶面喷施乙烯利使棉花变得盐敏感,并抑制 OE-*GhTOPP6a* 幼苗的耐盐性。进一步研究发现 GhMYB4 能与 GhTOPP6a 的启动子结合,在盐胁迫下增加 GhTOPP6a 的转录水平,最终导致乙烯合成减少。GhMYB4 与 GhTOPP6a 的转录水平被乙烯抑制,进而正反馈调控乙烯的合成。总之,GhMYB4-GhTOPP6a-GhERF9 模块为揭示 PP1 蛋白磷酸酶调控乙烯生物合成增强棉花耐盐性研究提供了新的视角 (图 3)。

A Ghmyb4-Ghtopp6a-Gherf9 Module Regulates Salt Tolerance in Cotton (*Gossypium Hirsutum* L.) Through Inhibiting the Biosynthesis of Ethylene

Protein Phosphatase 1 (PP1) is an important protein phosphatase family in eukaryotes. With the vigorous development of genomics, more and more protein phosphatases are being identified and investigated in plants. However, the role of PP1 in plant resistance to abiotic stress has been rarely reported. In this study, we screened a cotton (*Gossypium hirsutum* L.) cDNA library using Virus-Induced Gene Silencing (VIGS) assay and identified a Type One Protein Phosphatase 6 (GhTOPP6a) in the PP1 family that positively regulates cotton salt tolerance. Consistently, OE-*GhTOPP6a* cotton plants showed salt tolerance; while, CRI-*GhTOPP6a* plants exhibited salt



sensitivity in cotton. In addition, GhTOPP6a interacted with and dephosphorylated Ethylene Response Factor 9 (GhERF9) on threonine 81 to negatively regulate the transcriptional activation activity of 1-aminocyclopropane-1-carboxylate oxidase 3 (*GhACO3*) promoter. Furthermore, we clarified that the transcription level of *GhACO3* is related to ethylene release, negatively regulating salt tolerance in cotton. Importantly, exogenous foliar application of ethephon inhibited the salt tolerance of cotton and compromised salt tolerance in OE-*GhTOPP6a* seedlings. We also found that GhMYB4 can bind to the promoter of *GhTOPP6a*, increasing transcription levels under salt stress, which ultimately led to the reduction of ethylene synthesis. Furthermore, the transcript levels of *GhMYB4* and *GhTOPP6a* are repressed by ethylene, which in turn positively feedback regulates ethylene synthesis. In conclusion, the GhMYB4-GhTOPP6a-GhERF9 module provides a new perspective for cotton salt tolerance via inhibition of ethylene biosynthesis (Figure 3).

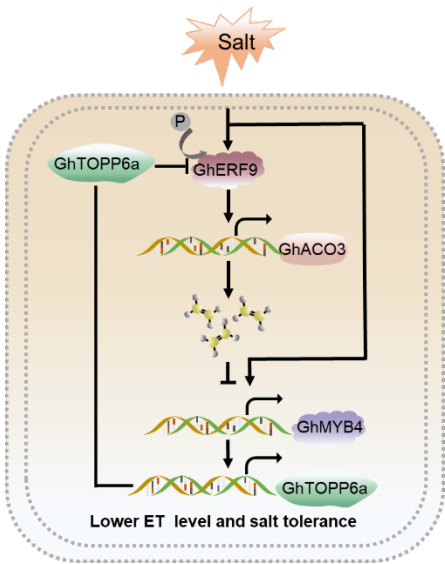


图 3、GhMYB4-GhTOPP6a-GhERF9 模块通过调控乙烯合成应答盐胁迫。

Figure 3. The GhMYB4-GhTOPP6a-GhERF9 module responds to salt stress by regulating ethylene synthesis.

4、陆地棉K⁺转运蛋白GhKUP3aD的功能鉴定和转录调控

钾(K⁺)是作物生长所必需的营养元素。K⁺转运蛋白对植物体内 K⁺的吸收和转运起着关键作用。拟南芥中大多数 K⁺转运蛋白已经得到了广泛的研究，但陆地棉中 K⁺转运体家族成员的功能仍有许多未知。从棉花 RNA-seq 数据中鉴定出编码高亲合 K⁺转运蛋白的基因 *GhKUP3aD*，发现 *GhKUP3aD* 在低 K⁺条件下对棉花 K⁺的吸收起重要作用。*GhKUP3aD* 属于陆地棉 HAK/KUP/KT 家族，低钾胁迫处理能够显著诱导 *GhKUP3aD* 的高表达。通过双靶点对 *GhKUP3aD* 进行 CRISPR 敲除材料的构建，同时构建了 *GhKUP3aD* 的超表达转基因材料(图 4A)。在低钾处理下，*GhKUP3aD* 敲除材料的生物量显著降低(图 4B)，且具有更加明显的缺钾症状(图 4C, D)，与 *GhKUP3aD* 过表达植株表现相反。使用 *GhKUP3aD* 转录起始位点上游 400 bp 的启动子序列对低钾诱导的 cDNA 文库进行筛选，得到了多个在酵母中与 *GhKUP3aD* 启动子互作的转录因子，其中包括一个 C2H2 型锌指蛋白



转录因子 GhSTZ1。双荧光素酶报告基因检测实验、凝胶迁移实验证实 GhSTZ1 能够直接与 GhKUP3aD 的启动子结合并正调控其表达(图 4E-G)。沉默 *GhSTZ1* 的棉花植株在低钾胁迫下具有更加明显的缺钾症状，表现较对照植株更低的 K⁺含量和 K⁺吸收速率 (图 4H-J)。

Functional Identification and Transcriptional Regulation of the K⁺ Transporter GhKUP3aD in Upland Cotton (*Gossypium hirsutum* L.)

Potassium (K⁺) is an essential nutrient for plant growth and crop production. K⁺ transporters play critical roles in the absorption and transport of K⁺ within plants. While most K⁺ transporters in *Arabidopsis* have been extensively studied, those in upland cotton have not yet been subjected to comprehensive research.

The GhKUP3aD encoding a high-affinity K⁺ transporter was identified from cotton RNA-seq data, proving that GhKUP3aD plays a crucial role in cotton's absorption of K⁺ under low K⁺ conditions. GhKUP3aD belongs to the HAK/KUP/KT family of upland cotton. Low K⁺ stress can significantly induce the high expression of *GhKUP3aD*. CRISPR knockout materials were constructed for *GhKUP3aD* through dual targets, and two overexpression transgenic lines for *GhKUP3aD* was constructed at the same time (Figure 4A). Under low K⁺ treatment, the biomass of *GhKUP3aD* knockout materials was significantly reduced (Figure 4B), and they had more obvious K⁺ deficiency symptoms (Figure 4C, D), which was opposite to the performance of *GhKUP3aD* overexpression plants. The 400 bp promoter sequence upstream of the *GhKUP3aD* transcription start site was used to screen the low potassium-induced cDNA library, and multiple transcription factors that interacted with the *GhKUP3aD* promoter in yeast were obtained, including a C2H2 zinc finger protein transcription factor GhSTZ1. Dual-luciferase reporter assay and electrophoretic mobility shift assay confirmed that GhSTZ1 can directly bind to the promoter of *GhKUP3aD* and positively regulate its expression (Figure 4E-G). Cotton plants silenced by *GhSTZ1* had more obvious symptoms of K⁺ deficiency, showing lower K⁺ content and lower K⁺ absorption rate than control plants (Figure 4H-J).

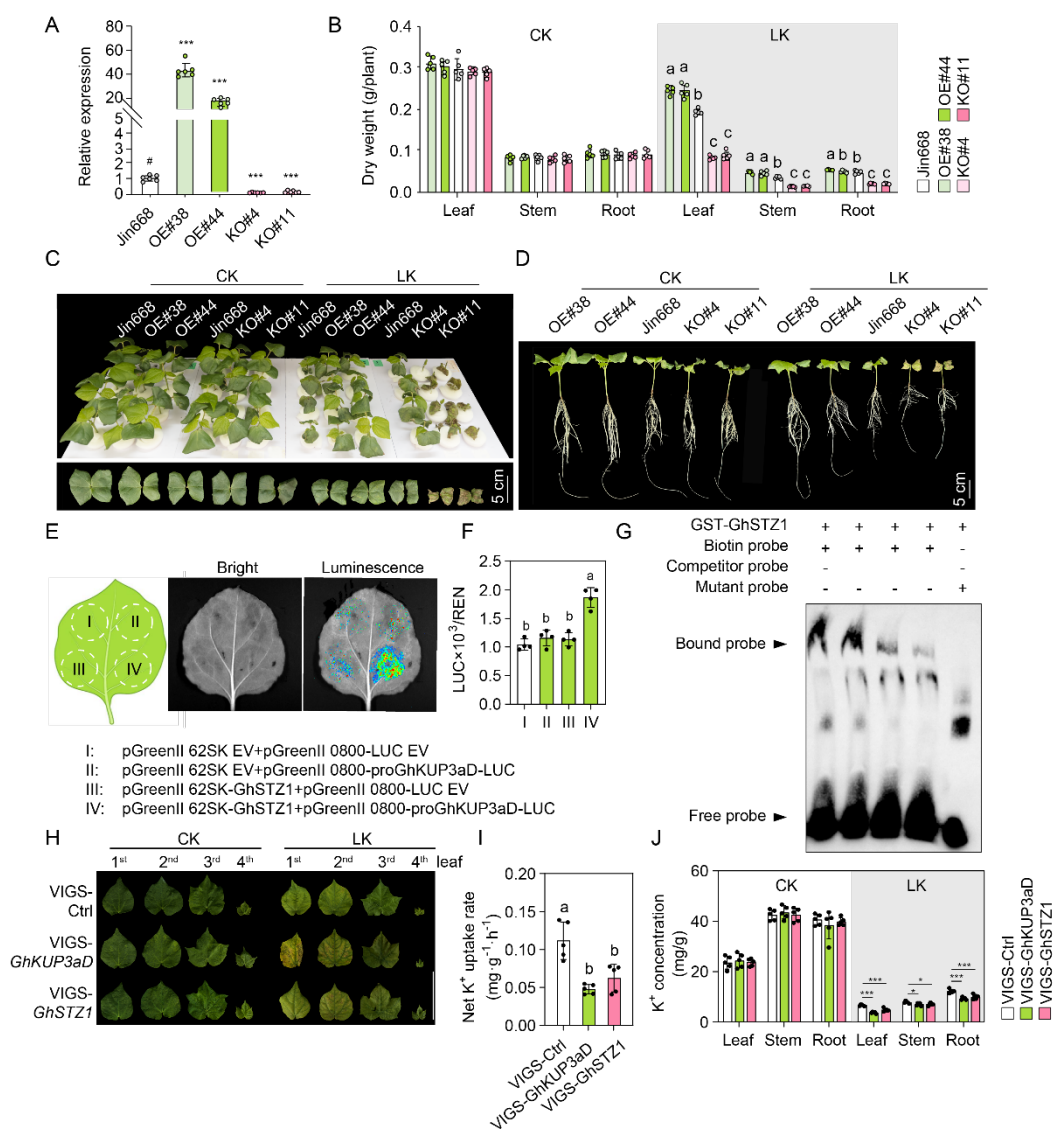


图 4、GhSTZ1-GhKUP3aD 正调控陆地棉 K⁺吸收。
Figure 4. GhSTZ1-GhKUP3aD positively regulates K⁺ uptake in upland cotton.

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

1. Zhao P#, Zhao M#, Gao X, Shan Y, Li F*, Tian X, Li Z (2024) GhWRKY1bD improves drought tolerance by co-regulation of ABA, ROS, and proline homeostasis in cotton (*Gossypium hirsutum*). *Ind Crop Prod* 220: 119179.
2. Abudurezike A, Liu X, Aikebaier G, Shawuer A*, Tian X* (2024) Effect of different irrigation and fertilizer coupling on the liquiritin contents of the licorice in Xinjiang arid area. *Ecol Indic* 158: 111451.



3. Xing J[#], Feng Y[#], Zhang Y, Wang Y, Li Z, Zhang M* (2024) Ethylene accelerates maize leaf senescence in response to nitrogen deficiency by regulating chlorophyll metabolism and autophagy. **Crop J** 12: 1391–1403.
4. Yao Q, Feng Y, Wang J, Zhang Y, Yi F, Li Z, Zhang M* (2024) Integrated metabolome and transcriptome analysis of gibberellins mediated the circadian rhythm of leaf elongation by regulating lignin synthesis in maize. **Int J Mol Sci** 25: 2705.

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(一) 研究进展

1、冠菌素介导茉莉酸和油菜素内酯信号调控玉米节间伸长的分子机制

倒伏影响了玉米的生长、发育和产量形成。较短的基部节间长度有利于提供玉米的抗倒伏性。油菜素类固醇(BRs)和茉莉酸(JA)通过拮抗调节玉米节间生长，但潜在的分子机制尚不清楚。在本研究中，冠菌素(COR)的应用抑制了拔节期玉米基部节间伸长，并抑制了细胞壁相关基因木葡聚糖内转葡萄糖基酶/水解酶 1(*ZmXTH1*)的表达，该基因在玉米植株中的过表达促进了节间伸长。我们证明了碱性螺旋-环-螺旋(bHLH)转录因子 *ZmbHLH154* 直接与 *ZmXTH1* 启动子结合并诱导其表达，而 bHLH 转录因子 *ILI1* 结合 BHLH 1(*ZmIBH1*)通过与 *ZmbHLH154* 形成异二聚体来抑制这种转录激活。过表达 *ZmbHLH154* 导致节间更长，而 *zmbhlh154* 突变体的节间比野生型短。JA 依赖性转录因子 *ZmMYC2-4* 和 *ZmMYC2-6* 与 BR 信号传导的关键因子 *ZmBZR1* 相互作用消除了 *ZmBZR1* 对其下游基因 *ZmIBH1* 的抑制作用。综上所述，这些结果揭示了 JA 通过减弱 BR 信号抑制 *ZmXTH1* 表达来调节 bHLH 网络，从而调节玉米节间伸长 (Wang et al., *Plant Physiol*, 2024)。

Molecular Mechanism of Coronatine Regulating Internode Elongation by Mediating Brassinosteroid Signaling in Maize

Lodging restricts growth, development, and yield formation in maize (*Zea mays* L.). Shorter internode length is beneficial for lodging tolerance. However, although brassinosteroids (BRs) and jasmonic acid (JA) are known to antagonistically regulate internode growth, the underlying molecular mechanism is still unclear. In this study, application of the JA mimic coronatine (COR) inhibited basal internode elongation at the jointing stage and repressed expression of the cell wall-related gene *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE 1* (*ZmXTH1*), whose overexpression in maize plants promoted internode elongation. We demonstrated that the basic helix-loop-helix (bHLH) transcription factor *ZmbHLH154* directly binds to the *ZmXTH1* promoter and induces its expression, whereas the bHLH transcription factor *ILI1* BINDING BHLH 1 (*ZmIBH1*) inhibits this transcriptional activation by forming a heterodimer with *ZmbHLH154*. Overexpressing *ZmbHLH154* led to longer internodes, whereas *zmbhlh154* mutants had shorter internodes than

the wild type. The core JA-dependent transcription factors ZmMYC2-4 and ZmMYC2-6 interacted with BRASSINAZOLE RESISTANT 1 (ZmBZR1), a key factor in BR signaling, and these interactions eliminated the inhibitory effect of ZmBZR1 on its downstream gene *ZmIBH1*. Collectively, these results reveal a signaling module in which JA regulates a bHLH network by attenuating BR signaling to inhibit *ZmXTH1* expression, thereby regulating cell elongation in maize (Wang et al., *Plant Physiol*, 2024).

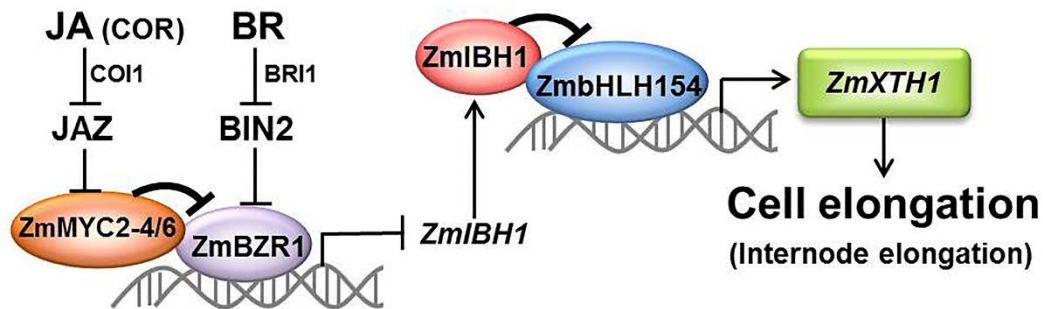


图1、冠菌素通过介导茉莉酸和油菜素内酯信号调控玉米节间伸长的分子机制。

Figure 1. Jasmonic acid affects maize internode elongation by regulating cell elongation through mediating the brassinosteroids pathway.

2、*ZmSCE1a* 通过增强 *GCN5* 稳定性提高玉米抗旱性

干旱胁迫对玉米的生长和产量构成严重威胁。然而，玉米抗旱性的分子基础尚不明确。在本研究中，发现一种 SUMO 化 E2 结合酶 *ZmSCE1a*，在玉米抗旱中发挥正向调控的作用。分子和生化分析表明，SUMO 化的 E3 连接酶 *ZmMMS21* 与 *ZmSCE1a* 共同作用，使组蛋白乙酰转移酶复合物 (*ZmGCN5*-*ZmADA2b*) SUMO 化。此外，*ZmGCN5* 的 SUMO 化可通过 26S 蛋白酶体途径增强 *GCN5* 的稳定性。此外，*ZmGCN5* 的过表达植株表现出耐旱的表型，表现出 O_2^- 积累的减少、丙二醛含量和离子渗透性的降低。此外，在干旱胁迫下，*ZmGCN5* 的过表达植株的胁迫响应基因和脱落酸 (ABA) 依赖基因的转录水平也显著上调。*ZmGCN5* 的过表达幼苗在干旱胁迫下增强了干旱诱导 ABA 的产生。综上所述，研究结果揭示了 *ZmSCE1a* 能增强 *ZmGCN5* 的稳定性，从而减轻干旱诱导的氧化损伤，进而增强玉米的干旱胁迫响应 (Feng et al., *Plant J*, 2024)。

ZmSCE1a Positively Regulates Drought Tolerance by Enhancing the Stability of *ZmGCN5*

Drought stress impairs plant growth and pose a serious threat to maize (*Zea mays*) production and yield. Nevertheless, the elucidation of the molecular basis of drought resistance in maize is still uncertain. In this study, we identified *ZmSCE1a*, a SUMO E2 conjugating enzyme, as a positive regulator of drought tolerance in maize. Molecular and biochemical assays indicated that E3 SUMO ligase *ZmMMS21* acts together with *ZmSCE1a* to SUMOylate histone acetyltransferase

complexes (ZmGCN5-ZmADA2b). SUMOylation of ZmGCN5 enhances its stability through the 26S proteasome pathway. Furthermore, *ZmGCN5*-overexpressing plants showed drought tolerance performance. It alleviated O₂⁻ accumulation, malondialdehyde (MDA) content, and ion permeability. What's more, the transcripts of stress-responsive genes and ABA-dependent genes were also significantly upregulated in *ZmGCN5*-overexpressing plants under drought stress. Overexpression of *ZmGCN5* enhanced drought-induced ABA production in seedlings. Taken together, our results indicate that ZmSCE1a enhances the stability of ZmGCN5, thereby alleviating drought-induced oxidative damage and enhancing drought stress response in maize (Feng et al., *Plant J*, 2024).

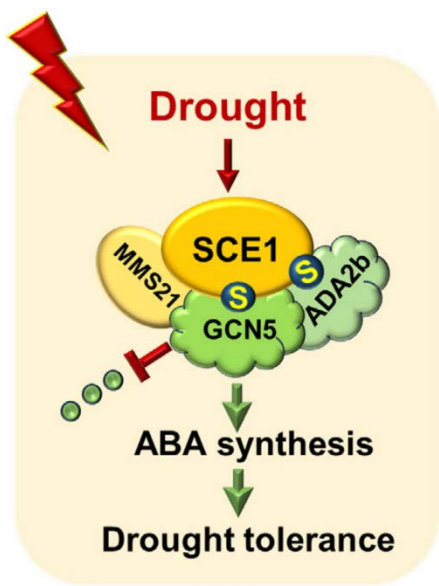


图2、ZmSCE1a增强ZmGCN5稳定性调控玉米抗旱的分子机制。
Figure 2. The molecular mechanism by which ZmSCE1a enhances ZmGCN5 stability to regulate drought tolerance.

3、玉米籽粒脱水的主要途径以及驱动机制研究

玉米籽粒脱水慢严重影响其机械化收获。本研究通过去除苞片或穗上部分，在苞片或穗上涂抹凡士林，分析了籽粒、胚、胚乳、苞片、穗轴和穗柄含水量的变化及其相关性，明确了影响籽粒脱水的关键穗指标和主要驱动力。通过对活性染料碱性品红在玉米茎、穗柄、穗轴和籽粒中的流动情况的观察，阐明了玉米穗内水分交换和籽粒水分流失的途径。结果表明：吐丝后 5-20 d，水在穗轴和穗柄之间双向流动，同时有输入和输出；吐丝 30-40 天后，水分主要由穗轴和穗柄净输出，籽粒脱水的驱动力是灌浆和水分回流。在吐丝后 50-60 天的物理脱水阶段，水分再次在穗轴和穗柄内双向流动，籽粒脱水的驱动力转向籽粒和苞片表面的物理蒸发和水分回流。因此，在灌浆和物理脱水阶段，籽粒中的水分可以通过花梗、穗轴和穗柄回到植株中重复利用，这为籽粒脱水的研究提供了新的理论依据。



Investigation into the Key Pathways and Driving Mechanisms of Maize Grain Dehydration

This study analyzed changes and correlations in water content across grains, embryos, endosperm, bracts, cobs, and ear-stalks. Experimental treatments included bracts or upper parts of ears removal and petroleum jelly application to bracts or grains to inhibit evaporation. Key ear indices and the main driving forces influencing grain dehydration were identified. The flow of the mobile dye basic fuchsin in stems, ear-stalks, cobs, and grains was observed, elucidating water exchange within the ear and water loss from the grains. Results indicated bidirectional water flow between the cob and ear-stalk, with both influx and efflux occurring from 5 to 20 days after silking. From 30 to 40 days after silking, during the slow filling stage, water primarily exhibited net outflow from the cob and ear-stalk. The driving forces for grain dehydration included filling processes and water reflux. During the physical dehydration stage (50–60 days after silking), water flow in the cob and ear-stalk became bidirectional again. The primary driving forces for grain dehydration shifted to physical evaporation and water reflux from the grain and bract surfaces. Thus, during the filling and physical dehydration stages, grain water can be recycled within the plant via the peduncle, cob, and ear-stalk. This finding offers a novel theoretical framework for understanding grain dehydration.

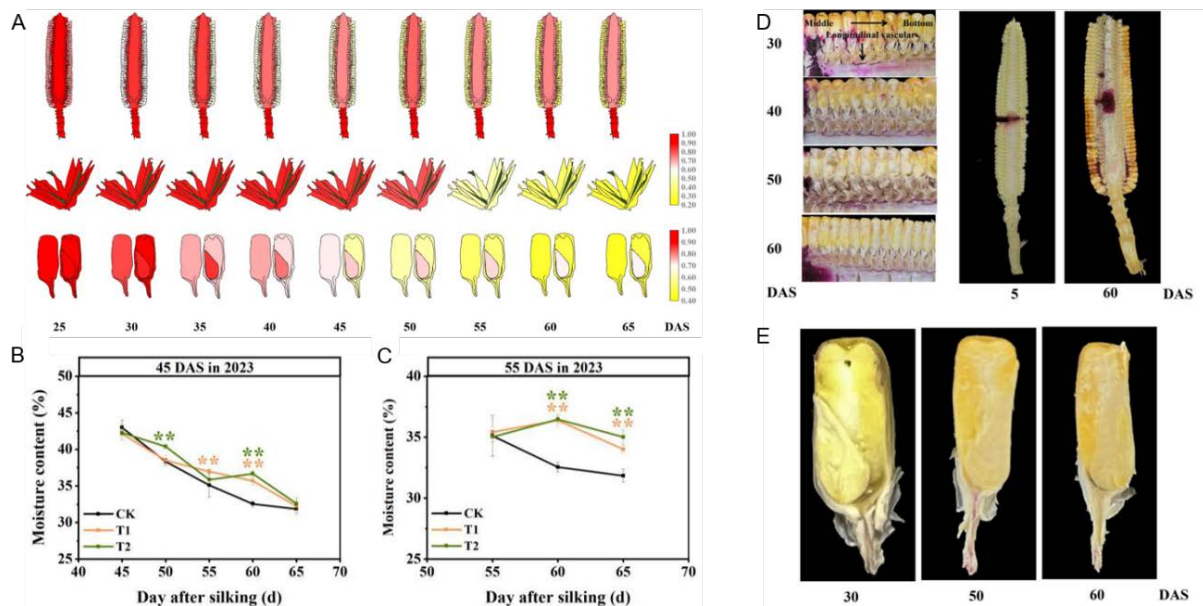


图3、玉米籽粒不同时期通过调整籽粒灌浆、苞叶和籽粒表面蒸发以及水分回流的强度影响籽粒脱水。

Figure 3. The dehydration of maize grains was affected by adjusting the intensity of grain filling, bract and grain surface evaporation, and water reflux in different periods.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Peng C, Xu H, Xie S, Zhong X, Chen L, He Y, Li Z, Zhou Y*, Duan L (2024) Unveiling the regulatory role of miRNAs in internode elongation: integrated analysis of microRNA and mRNA expression profiles across diverse dwarfing treatments in maize (*Zea mays* L.). **J Agric Food Chem** 72(13):7533-7545.
2. Wang X, Ren Z, Xie S, Li Z, Zhou Y*, Duan L* (2024) Jasmonate mimic modulates cell elongation by regulating antagonistic bHLH transcription factors via brassinosteroid signaling. **Plant Physiol** 195(4):2712-2726.
3. Feng T, Wang Y, Zhang M, Zhuang J, Zhou Y*, Duan L* (2024) ZmSCE1a positively regulates drought tolerance by enhancing the stability of ZmGCN5. **Plant J** DOI: 10.1111/tpj.17103. Epub ahead of print. PMID: 39462465.
4. Jiang B, Yang J, Zhong X, Yan S, Yin M, Shen J, Lei B, Li Z, Zhou Y*, Duan L* (2024) Triacanol delivery by nano star shaped polymer promoted growth in maize. **Plant Physiol and Bioch** 213: 108815 .
5. Du L, Li X, Ding Y, Ma D, Yu C, Duan L* (2024) Design, synthesis, and bioactivities of N-heterocyclic ureas as strigolactone response antagonists against parasitic-weed seed germination. **J Agric Food Chem** PMID: 38593208.
6. Du L, Li X, Ding Y, Ma D, Yu C, Zhao H, Wang Y, Liu Z, Duan L* (2024) Design, synthesis and biological evaluation of novel phenyl-substituted naphthoic acid ethyl ester derivatives as strigolactone receptor inhibitor. **Int J Mol Sci** 25(7):3902.
7. Jie Y#, Wang W#, Wu Z#, Ren Z, Li L, Zhou Y, Zhang M, Li Z, Yi F*, & Duan L* (2024) Deciphering physiological and transcriptional mechanisms of maize seed germination. **Plant Mol Biol** 114(5): 94.

专利申请与授权:

段留生, 王春英, 于春欣, 赵汗青, 郭兵博, 杜琳, 王兴, 周于毅, 姜峰, 李召虎, 谭伟明; 具有独脚金内酯活性的苯乙酯烯醚内酯类化合物及其制备与应用; 专利申请号: CN114874165B; 申请日期: 2024 年 3 月 6 日。

(三) 研究队伍

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李继刚
课题组

李继刚，教授。青年创新人才项目(2014)，国家杰出青年科学基金获得者(2022)。

研究方向：光调控植物逆境响应的分子机制，以及植物避荫反应的分子调控机制。

(一) 研究进展

1、“智慧株型”基因调控玉米上部叶夹角的分子机制 (与田丰教授课题组合作)

玉米是全球和我国的第一大粮食作物，种植密度的不断增加是玉米单产水平持续提升的关键因素之一。因此，发掘和利用耐密高产基因、培育耐密高产品种是提高我国玉米单产水平的重要途径。前期在田间鉴定到一个上部叶夹角紧凑、中下部叶夹角相对舒展的自然突变体材料，具有“上紧下松”的智慧株型特征，命名为*leaf angle architecture of smart canopy 1 (lac1)*。*LAC1*编码类固醇C-22羟化酶 (DWF4)，其外显子上的一个转座子插入导致编码蛋白提前终止。在高密度种植条件下，携带*lac1*突变等位基因的“上紧下松”株型可以显著增加群体中下部冠层透光率、增强穗位叶净光合速率、削弱密植群体的避荫反应，最终促进玉米群体产量显著增加。研究结果表明，调控玉米叶夹角的关键转录因子RAVL1能够直接激活*LAC1*的表达，从而控制玉米叶环区油菜素内酯的积累，最终影响玉米叶夹角的大小。RAVL1仅能与phyA互作，而不能与phyB互作。随着种植密度增加，红光:远红光的比例 (R/FR) 降低，促进phyA蛋白积累，phyA与RAVL1互作并促进RAVL1蛋白的降解，从而削弱RAVL1对*LAC1*的激活作用，最终减小高密度条件下的玉米叶夹角。在*lac1*突变体中，phyA-RAVL1介导的光信号通路被阻断，从而削弱*lac1*突变体对遮荫的响应。综上，一方面*lac1*“上紧下松”的株型特征优化了冠层内的光分布、增强了密植群体的光合效率，另一方面*lac1*对遮荫响应的削弱增强了耐荫性，因此*lac1*形态的改良和生理的适应协同促进了密植增产 (Tian et al., *Nature*, 2024)。

Maize Smart-Canopy Architecture Enhances Yield at High Densities

(in collaboration with Prof. Feng Tian's lab)

Increasing planting density is a key strategy for enhancing maize yields. An ideotype for dense planting requires a ‘smart canopy’ with leaf angles at different canopy layers differentially optimized to maximize light interception and photosynthesis, among other features. Here we identified *leaf angle architecture of smart canopy 1 (lac1)*, a natural mutant with upright upper leaves, less erect middle leaves and relatively flat lower leaves. *lac1* has improved photosynthetic capacity and attenuated responses to shade under dense planting. *LAC1* encodes a brassinosteroid C-22

hydroxylase that predominantly regulates upper leaf angle. Phytochrome A photoreceptors accumulate in shade and interact with the transcription factor RAVL1 to promote its degradation via the 26S proteasome, thereby inhibiting activation of *LAC1* by RAVL1 and decreasing brassinosteroid levels. This ultimately decreases upper leaf angle in dense fields. Large-scale field trials demonstrate that *lac1* boosts maize yields under high planting densities. To quickly introduce *lac1* into breeding germplasm, we transformed a haploid inducer and recovered homozygous *lac1* edits from 20 diverse inbred lines. The tested doubled haploids uniformly acquired smart-canopy-like plant architecture. We provide an important target and an accelerated strategy for developing high-density-tolerant cultivars, with *lac1* serving as a genetic chassis for further engineering of a smart canopy in maize (Tian et al., *Nature*, 2024).

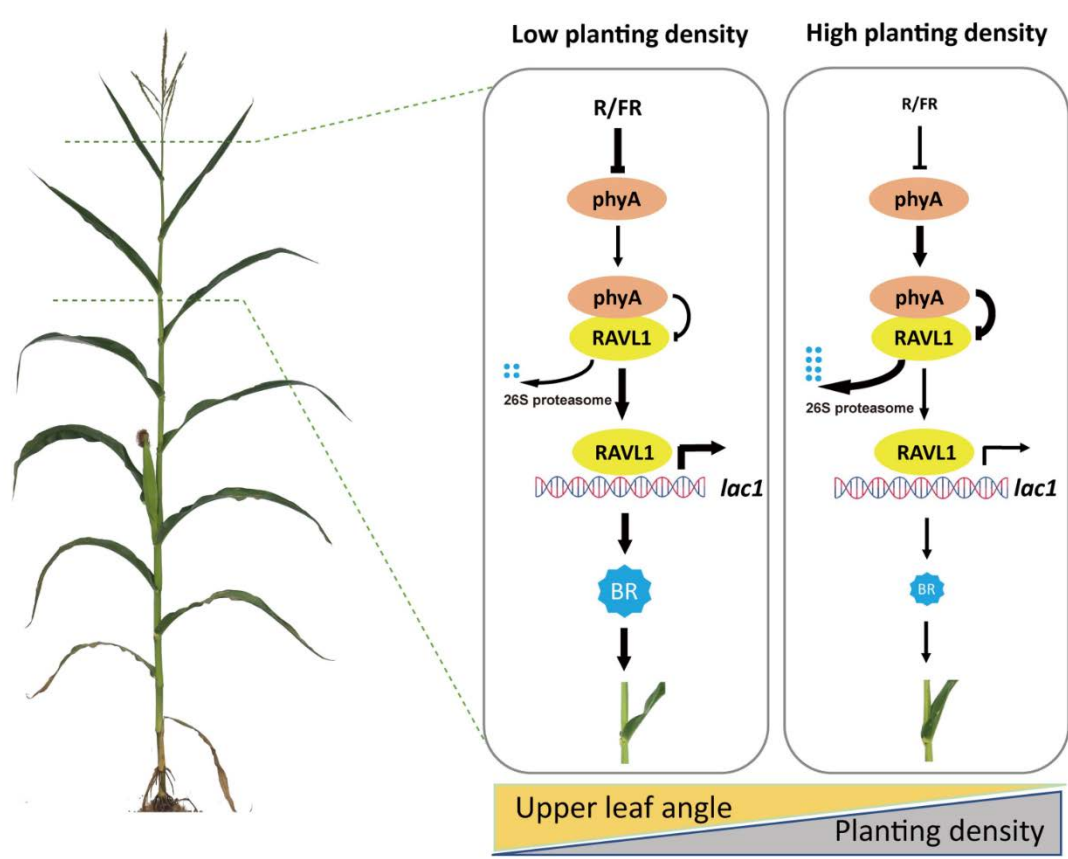


图 1、在不同种植密度下 *lac1* 调控玉米上部叶夹角的工作模型。

Figure 1. Model for how *lac1* responds to varying light signals to dynamically regulate upper leaf angle as planting density increases.

2、植物远红光受体 phyA 的蛋白磷酸化机制

phyA 是植物唯一能在远红光下起始光信号转导的光受体。四十多年前，人们就发现燕麦 phyA 在体内能够被磷酸化，但是至今仍未鉴定出能够特异磷酸化 phyA 的蛋白激酶。2018 年，李继刚课题组在拟南芥中鉴定到远红光信号传递的新组分 TANDEM ZINC-FINGER/PLUS3 (TZP)，发现 TZP



能够与 phyA 相互作用并且调控 phyA 在体内的蛋白磷酸化。进一步研究表明，磷酸化的 phyA 可能是活性更强的形式，在远红光信号转导中发挥重要功能。该研究发现，蛋白激酶 PHOTOREGULATORY PROTEIN KINASES (PPKs, 也被称作 MUT9-LIKE KINASES) 能够与 phyA 直接互作，并且在体外、体内磷酸化 phyA。而 TZP 的 N 端含有两个内在无序区 (intrinsically disordered regions, IDRs)，TZP 在植物照射远红光后能够在体内形成核内小体 (nuclear bodies, NBs)。该研究随后证明 TZP 在体内、体外确实能够发生液-液相分离，并且两个 IDRs 都是 TZP 液-液相分离所必需的。免疫共沉淀实验结果表明，TZP 能够促进 phyA 和 PPK1 的相互作用。而激光共聚焦显微镜观察结果显示，在植物细胞中共表达 PPKs 和 phyA 时，它们在细胞核中只形成较小的 NBs 且不能共定位，而同时表达 TZP 后，PPKs 和 phyA 均共定位于 TZP 形成的较大 NBs 中。此外，该研究把 TZP 的 IDRs 替换为人 FUS 蛋白的 IDR 结构域，结果显示该人工 TZP 能够与野生型 TZP 一样完全回补 *tzp* 突变体在远红光下长下胚轴的表型，而缺失 IDRs 的 TZP 则不能完全回补 *tzp* 突变体表型，表明 TZP IDRs 驱动的液-液相分离是 TZP 行使正常功能所必需的。综上，TZP 通过将 PPKs 和 phyA 招募到其液-液相分离形成的 NBs 中，促进它们的共定位和相互作用，从而增强 PPKs 对 phyA 的磷酸化。本研究鉴定到第一类能够磷酸化 phyA 的蛋白激酶 PPKs，并且阐明 TZP 通过液-液相分离促进 PPKs 磷酸化 phyA 的分子机制，为进一步深入解析远红光信号途径以及光信号调控网络提供了新的见解 (Feng et al., *Nat Plants*, 2024)。

Liquid-Liquid Phase Separation of TZP Promotes PPK-Mediated Phosphorylation of the Phytochrome A Photoreceptor

Phytochrome A (phyA) is the plant far-red (FR) light photoreceptor that plays an essential role in regulating photomorphogenic development in FR-rich conditions, such as canopy shade. It has long been observed that phyA is a phosphoprotein in vivo, however, the protein kinases that could phosphorylate phyA remain largely unknown. Here, we show that a small protein kinase family, consisting of four members named PHOTOREGULATORY PROTEIN KINASES (PPKs; also known as MUT9-LIKE KINASES [MLKs]), directly phosphorylate phyA in vitro and in vivo. In addition, TANDEM ZINC-FINGER/PLUS3 (TZP), a recently characterized phyA-interacting protein required for in vivo phosphorylation of phyA, is also directly phosphorylated by PPKs. We uncover that TZP contains two intrinsically disordered regions in its N-terminal domain that undergo liquid-liquid phase separation (LLPS) upon light exposure. Notably, the LLPS of TZP promotes colocalization and interaction between PPKs and phyA, thus facilitating PPKs-mediated phosphorylation of phyA in FR light. Together, our study identifies PPKs as the first class of protein kinases mediating phosphorylation of phytochrome A and demonstrates that the LLPS of TZP contributes significantly to more production of the phosphorylated phyA form in FR light (Feng et al., *Nat Plants*, 2024).

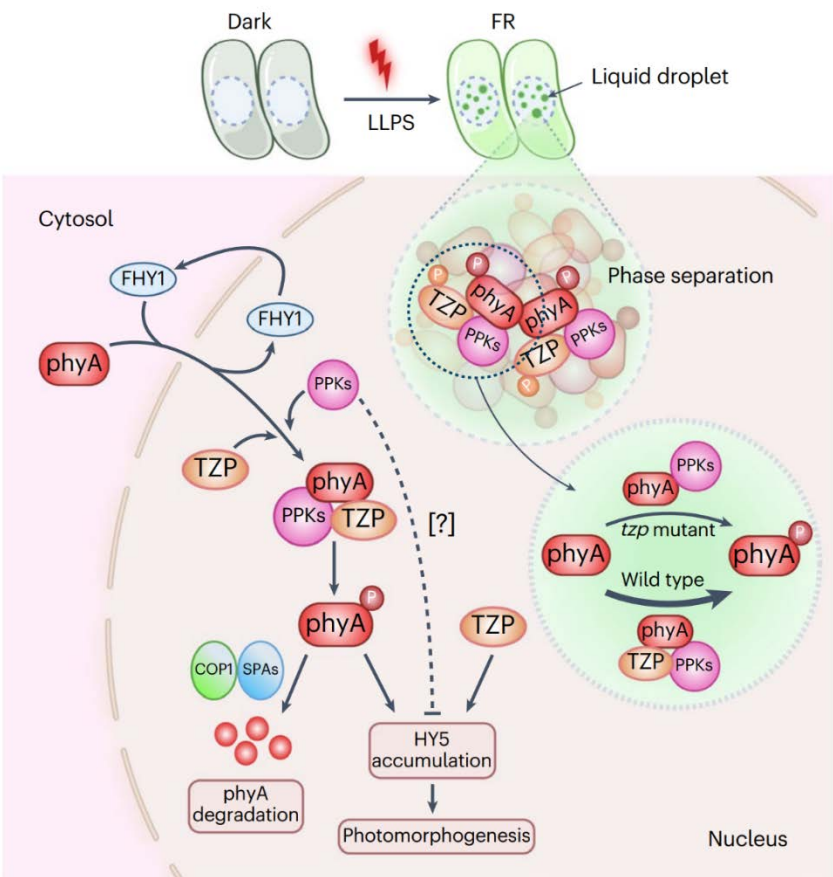


图2、TZP在远红光下通过液-液相分离促进PPKs对phyA磷酸化的分子模型。

Figure 2. The LLPS of TZP promotes PPK-mediated phosphorylation of phyA in FR light.

3、ABI4 调控蓝光信号转导的分子机制

ABSCISIC ACID-INSENSITIVE4 (ABI4) 编码一个 AP2/ERF 家族的转录因子，它最初是在筛选 ABA 不敏感突变体时被发现和鉴定的。该研究发现，在 2%的蔗糖浓度下，*abi4* 突变体在黑暗以及各种光条件下都发育出比野生型短的下胚轴，但是在无糖以及较低糖浓度 (0.3%) 下，*abi4* 突变体只在蓝光和白光下发育出较短的下胚轴，而在黑暗、红光和远红光下与野生型没有明显差异。这些结果表明 ABI4 在光形态建成中的调控角色受糖浓度调节。隐花色素 (cryptochromes, CRYs) 是介导蓝光下光形态建成的主要光受体。该研究结果表明 ABI4 与蓝光受体 CRY1/2 直接相互作用，且蓝光能够促进 ABI4 与 CRY1/2 的相互作用。PHYTOCHROME INTERACTING FACTOR 4 (PIF4) 是促进植物生长的转录因子，本研究结果显示 CRY1/2 在蓝光下能够显著抑制 PIF4 的蛋白积累，而 ABI4 通过抑制 CRY1/2 与 PIF4 的相互作用，增强 PIF4 在蓝光下的蛋白稳定性，从而促进幼苗在蓝光下的下胚轴伸长。此外，先前研究显示 ABI4 能够直接激活自身基因的表达，而该研究发现 CRY1/2 会增强 ABI4 对自身启动子的激活作用，但是 PIF4 通过与 ABI4 互作阻碍其对自身启动子的结合，从而抑制 ABI4 基因表达。综上，该研究表明 ABI4 与 PIF4 组成了一个分子模块，在调控 CRYs 介导的蓝光信号途径中发挥重要作用。由于 ABI4 在植物生长发育和环境响应等过程均发挥重要作用，



它可能作为光与其他内部和外部信号整合的一个关键节点，以优化植物对环境变化的适应性 (Song et al., *J Integr Plant Biol*, 2024)。

Regulation of Cryptochromes-Mediated Blue Light Signaling by the ABI4-PIF4 Module

ABSCISIC ACID-INSENSITIVE 4 (ABI4) is a pivotal transcription factor that coordinates multiple aspects of plant growth and development as well as plant responses to environmental stresses. ABI4 has been shown to be involved in regulating seedling photomorphogenesis, however, the underlying mechanism remains elusive. Here, we show that the role of ABI4 in regulating photomorphogenesis is generally regulated by sucrose, but ABI4 promotes hypocotyl elongation of *Arabidopsis* seedlings under blue (B) light under all tested sucrose concentrations. We further show that ABI4 physically interacts with PHYTOCHROME INTERACTING FACTOR 4 (PIF4), a well-characterized growth-promoting transcription factor, and post-translationally promotes PIF4 protein accumulation under B light. Further analyses indicate that ABI4 directly interacts with the B light photoreceptors cryptochromes (CRYs) and inhibits the interactions between CRYs and PIF4, thus relieving CRYs-mediated repression of PIF4 protein accumulation. In addition, while ABI4 could directly activate its own expression, CRYs enhance, whereas PIF4 inhibits ABI4-mediated activation of the *ABI4* promoter. Together, our study demonstrates that the ABI4-PIF4 module plays an important role in mediating CRYs-induced B light signaling in *Arabidopsis* (Song et al., *J Integr Plant Biol*, 2024).

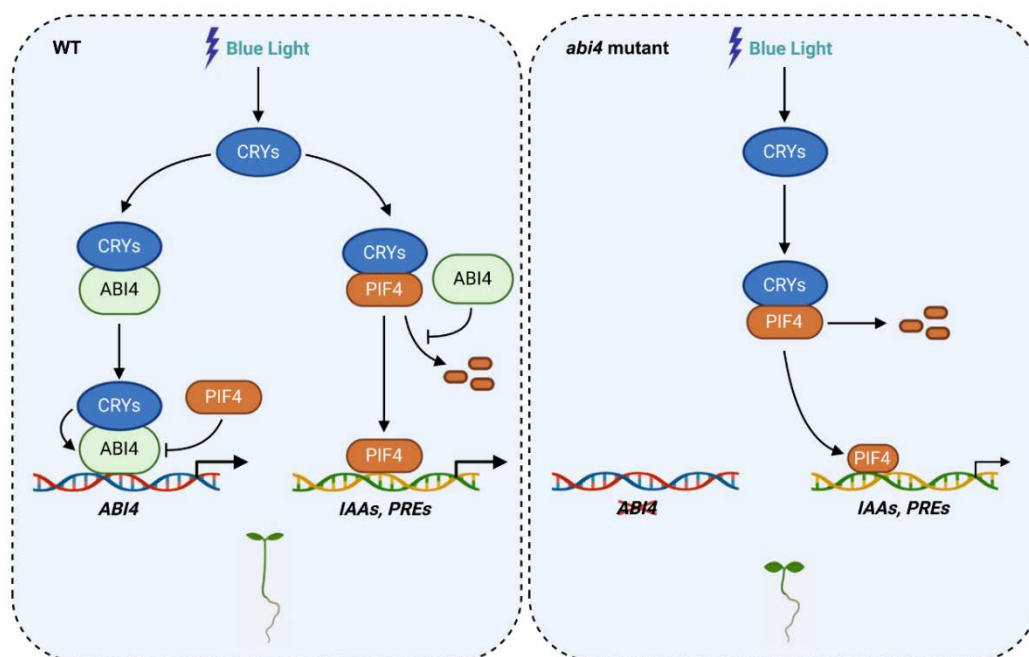


图3、ABI4调控CRYs介导的蓝光信号途径的工作模式图。

Figure 3. A working model depicting that ABI4 regulates CRYs-mediated blue light signaling.



4、玉米 phyA 的分子鉴定及功能分析

在玉米中有两个 phyA 光受体蛋白 (ZmphyA1 和 ZmphyA2), 但是其在玉米生长发育中的调控功能目前知之甚少, 本研究对玉米 phyA 进行了分子鉴定和功能分析。结果表明, 与拟南芥 phyA 类似, *ZmPHYA1/2* 的转录水平受光抑制, ZmphyA1/2 蛋白在红光和白光照射下迅速降解, 并且照光后 ZmphyA1/2 均能进入细胞核。然而, 和拟南芥 phyA 只与 PIF1 和 PIF3 互作不同的是, ZmphyA1/2 能够与几乎所有的玉米 PIFs 蛋白相互作用。ZmphyA1/2 双突变体在远红光下的中胚轴长度与黑暗下相近, 表明 ZmphyA1/2 确实是玉米感知远红光的主要光受体。但是, 与拟南芥 phyA 突变体在白光和红光下无明显表型不同的是, 玉米 ZmphyA1/2 双突变体在这些光照条件下均表现出中胚轴显著增长的表型, 这表明 ZmphyA 在光调控玉米生长发育中发挥独特的功能。此外, 田间实验数据显示, 成熟 ZmphyA1/2 双突变体的株高显著增加, 表明 ZmphyA 在玉米重要农艺性状的调控中扮演着关键角色。综上, 该研究结果显示 ZmphyA 与 AtphyA 具有相似的生化性质和保守功能, 但同时也表明 ZmphyA 在玉米的生长发育中发挥独特且重要的调控功能。该研究为深入理解单子叶植物的光信号转导机制提供了新的见解, 也为耐密植玉米新品种的培育提供了理论支持 (Cao et al., *Plant Physiol*, 2024)。

Molecular Characterization and Functional Analyses of the Maize Phytochrome A Photoreceptors

Maize (*Zea mays*) is one of the most important staple crops globally. To increase the yield, maize is planted at high densities, leading to mutual shading and the enrichment of far-red (FR) light in the shade. Phytochrome A (phyA) is the predominant photoreceptor in plants that initiates photomorphogenic development under FR light. In maize, there are two phyA photoceptors, named ZmphyA1 and ZmphyA2, but their functions remain largely obscure. In this study, we performed molecular characterization and functional analyses of the maize phyA photoreceptors. Similar to *Arabidopsis* phyA, both *ZmPHYA1* and *ZmPHYA2* transcript levels are repressed by light, ZmphyA proteins are rapidly degraded in response to red (R) and white (W) light, and both ZmphyA1 and ZmphyA2 translocate into the nucleus upon FR and R light exposure. However, in contrast to *Arabidopsis* phyA that only physically interacts with PHYTOCHROME-INTERACTING FACTOR1 (PIF1) and PIF3, both ZmphyA1 and ZmphyA2 were shown to directly interact with almost all maize PIF proteins. Moreover, although *Arabidopsis* phyA mutants displayed no obvious phenotypes compared to wild-type seedlings under W and R light, *ZmphyA1 ZmphyA2* double mutant seedlings developed significantly longer mesocotyls under these light conditions. Further, the height of mature *ZmphyA1 ZmphyA2* plants was significantly increased in the field experiments. Together, our study uncovers an important role of ZmphyAs in light control of maize growth and development, providing insights into the cultivation of new maize varieties with enhanced tolerance to high-density planting (Cao et al., *Plant Physiol*, 2024).

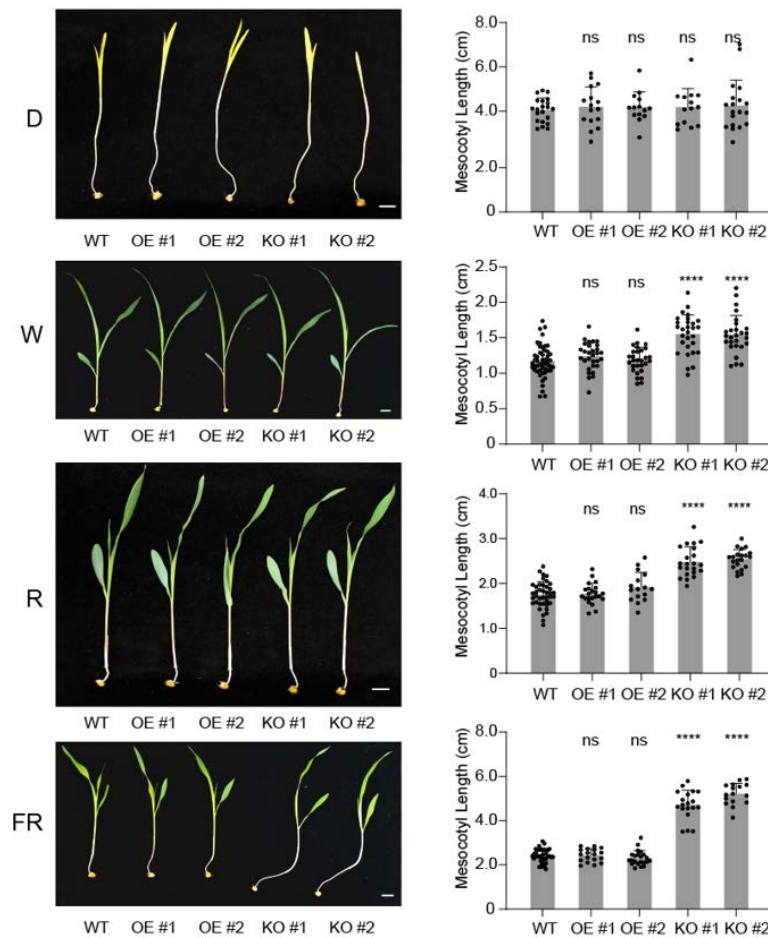


图4、*ZmphyA1/2*双突变体幼苗在黑暗(D)、白光(W)、红光(R)和远红光(FR)下的表型。

Figure 4. Phenotypes of *ZmphyA1/2* double mutant seedlings grown in darkness (D), white (W), red (R) and far-red (FR) light conditions.

5、综述植物协同响应遮荫和环境胁迫的分子机制

在密度种植下植物除了要应对遮荫胁迫，还可能同时面对包括非生物胁迫（如盐、干旱和极端温度）和生物胁迫（如病原体和害虫）在内的环境胁迫。因此，深入解析植物协同响应遮荫和环境胁迫的分子机制，有助于进一步理解植物环境适应性和发育可塑性的调控机理，为培育抗逆、高产的作物新品种提供理论依据和基因靶点。

李继刚和郭岩团队应邀撰写综述，系统总结了近年来关于植物协同响应遮荫和环境胁迫分子机制的研究进展。文章主要从三个方面进行了系统性总结：1) 植物感知和适应遮荫信号的关键调控组分及信号转导通路；2) 植物协同响应遮荫和非生物胁迫（包括盐、干旱、水淹、土壤养分缺乏和极端温度等）的分子机制；3) 植物协同响应遮荫和生物胁迫（包括病原体和害虫）的分子策略。该论文还提出了该领域亟待研究的重要科学问题 (Han et al., *Plant J*, 2024)。



Molecular Mechanisms Underlying Coordinated Responses of Plants to Shade and Environmental Stresses

Plants have evolved sophisticated mechanisms to simultaneously deal with multiple environmental stresses. This review summarizes recent major advances in our understanding of how plants coordinately respond to shade and environmental stresses, and discusses the important questions for future research. A deep understanding of how plants synergistically respond to shade together with abiotic and biotic stresses will facilitate the design and breeding of new crop varieties with enhanced tolerance to high-density planting and environmental stresses (Han et al., *Plant J*, 2024).

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

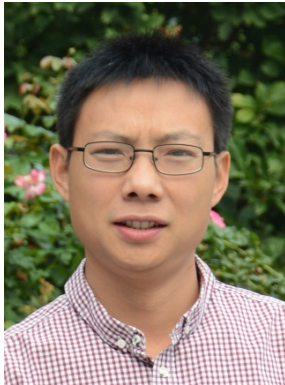
1. Tian J[#], Wang C[#], Chen F[#], Qin W, Yang H, Zhao S, Xia J, Du X, Zhu Y, Wu L, Cao Y, Li H, Zhuang J, Chen S, Zhang H, Chen Q, Zhang M, Deng X, Deng D, Li J*, Tian F* (2024) Maize smart-canopy architecture enhances yield at high densities. *Nature* 632: 576-584.
2. Feng Z[#], Wang M[#], Liu Y, Li C, Zhang S, Duan J, Chen J, Qi L, Liu Y, Li H, Wu J, Liu Y, Terzaghi W, Tian F, Zhong B, Fang X, Qian W, Guo Y, Deng X, Li J* (2024) Liquid-liquid phase separation of TZP promotes PPK-mediated phosphorylation of the phytochrome A photoreceptor. *Nat Plants* 10: 798-814.
3. Song P[#], Yang Z[#], Wang H[#], Wan F, Kang D, Zheng W, Gong Z, Li J* (2024) Regulation of cryptochrome-mediated blue light signaling by the ABI4-PIF4 module. *J Integr Plant Biol* 66: 2412-2430.
4. Cao Y[#], Zhang D[#], Li B, Li H, Qin X, Tian J, Wang C, Wang M, Han R, Qi L, Peng J, Zhao X, Zhang D, Zhao X, Chen L, Kang D, Tian F, Li J* (2024) Molecular characterization and functional analyses of maize phytochrome A photoreceptors. *Plant Physiol* 194: 2213-2216.
5. Han R[#], Ma L[#], Terzaghi W, Guo Y, Li J* (2024) Molecular mechanisms underlying coordinated responses of plants to shade and environmental stresses. *Plant J* 117: 1893-1913.
6. Peng J, Dong X, Yang S, Li J* (2024) Assessing the function of CBF1 in modulating the interaction between phytochrome B and PIF4. *Methods Mol Biol* 2795: 183-194.
7. Liu H, Li J (2024) Plant photobiology: From basic theoretical research to crop production improvement. *J Integr Plant Biol* 66: 847-848.

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研究方向：玉米抗盐碱的分子机理及生物育种。

(一) 研究进展

综述了植物耐盐碱的分子和遗传调控机制

郭岩和蒋才富团队受邀联合撰写综述，概述了目前植物耐盐分子机理的研究进展。论文重点阐述了渗透胁迫、盐离子转运和区隔化、氧化胁迫、碱性胁迫以及生长与耐盐性之间的权衡等方面的研究进展。论文还梳理了水稻、小麦、玉米和大豆中耐盐碱 QTL 基因克隆和功能研究进展，讨论了设计耐盐作物的可能策略和挑战 (Liang et al., *J Integr Plant Biol*, 2024)。

Designing Salt Stress-Resilient Crops: Current Progress and Future Challenges

This review summarizes our current knowledge of plant salt tolerance, emphasizing advances in elucidating the molecular mechanisms of osmotic stress tolerance, salt-ion transport and compartmentalization, oxidative stress tolerance, alkaline stress tolerance, and the trade-off between growth and salt tolerance. The manuscript also summarizes recent advances in understanding natural variation in the salt tolerance of crops and discuss possible strategies and challenges for designing salt stress-resilient crops.

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

1. Liang X#, Li J#, Yang Y*, Jiang C* and Guo Y* (2024) Designing salt stress-resilient crops: Current progress and future challenges. *J Integr Plant Biol* 66: 303-329.
2. Wang L#, Wang Y, Yin P, Jiang C* and Zhang M* (2024) ZmHAK17 encodes a Na⁺-selective transporter that promotes maize seed germination under salt conditions. *New Crops* 1:100024.
3. Liang X, Jiang C* (2024) Coping with salt stress. *Elife* 13: e101732.

专利授权：

蒋才富，尹攀，张敬波：一种耐受氯离子毒害的玉米抗盐 QTL 基因及其应用；专利号：

ZL202310232675.4；授权公告日：2024 年 10 月 22 日。



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研究方向：植物/作物根可塑性生长发
育的分子调控机制。

(一) 研究进展

铁氧还蛋白调控玉米氮利用效率的分子机制

氮(N)是植物生长发育并最终影响产量的一种必需大量营养素。因此，明确玉米(*Zea mays* L.)氮利用效率背后的遗传机制极为重要。硝酸盐(NO_3^-)是玉米偏好的无机氮源，我们针对低 NO_3^- 条件下玉米幼苗地上部 NO_3^- 积累情况开展了全基因组关联分析，确定了铁氧还蛋白家族成员ZmFd4是调控 NO_3^- 含量的主要因子。ZmFd4在叶绿体中表达，可以与亚硝酸还原酶(ZmNiRs)相互作用，并且促进ZmNiRs的活性。进一步研究发现，ZmFd4与其亲缘关系最近的同源基因ZmFd9能够形成高亲和力的异源二聚体。有趣的是，尽管ZmFd4发挥着与ZmFd9相似的生物学功能，二者均可以促进ZmNiRs的活性。然而，由于ZmFd4和ZmFd9具有更高的亲和力，因此ZmFd4和ZmFd9的相互作用限制了它们各自结合并刺激ZmNiRs活性的能力。ZmFd4基因敲除株系的 NO_3^- 含量降低，表现出更高效的 NO_3^- 同化能力，并且田间试验表明，在氮缺乏条件下，ZmFd4突变体的氮利用效率和籽粒产量也高于野生型。因此，我们的研究工作从分子和机制的层面为玉米氮高效自然变异提供了见解，有助于推进玉米乃至其他作物氮高效的遗传改良。该研究结果已经整理成论文，目前正在《Nature Plants》的修改稿中。

Ferredoxin-Mediated Mechanism for Efficient Nitrogen Utilization in Maize

Nitrogen (N) is an essential macronutrient for plant development and ultimately yield. Identifying the genetic components and mechanism underlying N use efficiency in maize (*Zea mays* L.) is thus of a great importance. Nitrate (NO_3^-) is a preferred inorganic N source in maize. Here, we performed a genome-wide association study for shoot NO_3^- accumulation in maize seedlings under low- NO_3^- conditions, identifying the ferredoxin family gene *ZmFd4*, as a major contributor to this trait. ZmFd4 interacts and colocalizes with nitrite reductases (ZmNiRs) in chloroplasts to promote their enzymatic activity. It forms a high-affinity heterodimer with its closest paralog, ZmFd9 in NO_3^- -sensitive manner. Although ZmFd4 exerts similar biochemical functions to ZmFd9, ZmFd4



and ZmFd9 interaction limits their ability to associate and stimulate activity of ZmNiRs. *ZmFd4* knockout lines with decreased NO_3^- contents exhibit more efficient NO_3^- assimilation and field experiments show consistently improved N utilization and grain yield under N-deficient conditions. Our work thus provides molecular and mechanistic insights into the natural variation in N utilization instrumental for genetic improvement of yield in maize and, potentially, other crops.

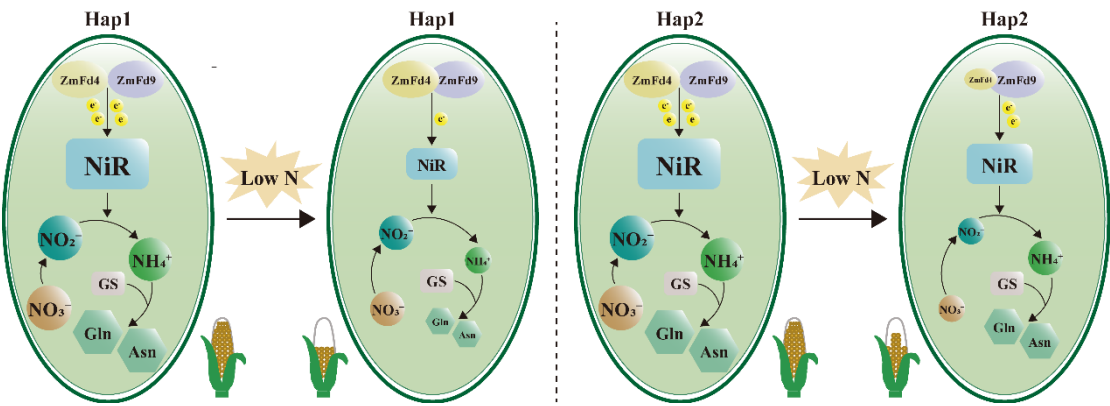


图1、铁氧还蛋白ZmFd调控硝态氮同化以及玉米籽粒产量的分子模型。

Figure 1. Conceptual model of ZmFd-mediated NO_3^- assimilation and maize grain yield in response to low N availability.

(二) 研究成果

专利授权：

1. 张静，贾冠南，陈国经纬；一种玉米氮高效利用基因及其分子标记和应用；专利号：ZL202211562186.0；授权公告日：2024年10月22日。
2. 张静，赵雪米，王亚平；一个玉米氮利用相关基因 *ZNCRG2* 及其应用；专利号：ZL202211671933.4；授权公告日：2024年11月08日。

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**陈其军**

陈其军，教授。

课题组

研究方向：植物生物技术。

(一) 研究进展

新型引导编辑器 PE6 在水稻中的建立与应用

引导是一种基于 CRISPR/Cas 的精确基因组编辑技术，用于作物育种。最近，通过从三个不同来源进化和改造的反转录酶(RT)变体，生成了四种新型引导编辑器，分别命名为 PE6a–d。在本研究中，我们测试了四种 PE6 变体以及具有双 RT 模块的另外两种 PE6 构建体在转基因水稻(*Oryza sativa*)植物中的编辑效率。PE6c，使用来自酵母 Tf1 逆转录转座子的进化和改造的 RT 变体，产生了最高的引导编辑效率。与 PEmax 相比，PE6c 在 15 个基因的 18 个农艺重要目标位点上的平均编辑效率倍数变化超过了 3.5。我们还证明了使用两个 RT 模块来提高 prime 编辑效率的可行性。我们的结果表明，PE6c 或其衍生物将是单子叶植物中引导编辑的绝佳选择。此外，我们的发现为基于引导编辑的水稻品种育种，以增强农艺重要性状奠定了基础。

Development and Application of the Novel Prime Editor PE6 in Rice

Prime editing is a versatile CRISPR/Cas-based precise genome-editing technique for crop breeding. Four new types of prime editors named PE6a–d were recently generated using evolved and engineered reverse transcriptase (RT) variants from three different sources. In this study, we tested the editing efficiencies of four PE6 variants and two additional PE6 constructs with double RT modules in transgenic rice (*Oryza sativa*) plants. PE6c, with an evolved and engineered RT variant from the yeast Tf1 retrotransposon, yielded the highest prime-editing efficiency. The average fold change in editing efficiency of PE6c compared to PEmax exceeded 3.5 across 18 agronomically important target sites from 15 genes. We also demonstrated the feasibility of using two RT modules to improve prime-editing efficiency. Our results suggest that PE6c or its derivatives would be an excellent choice for prime editing in monocot plants. In addition, our findings lay a foundation for prime-editing-based breeding of rice varieties with enhanced agronomically important traits.

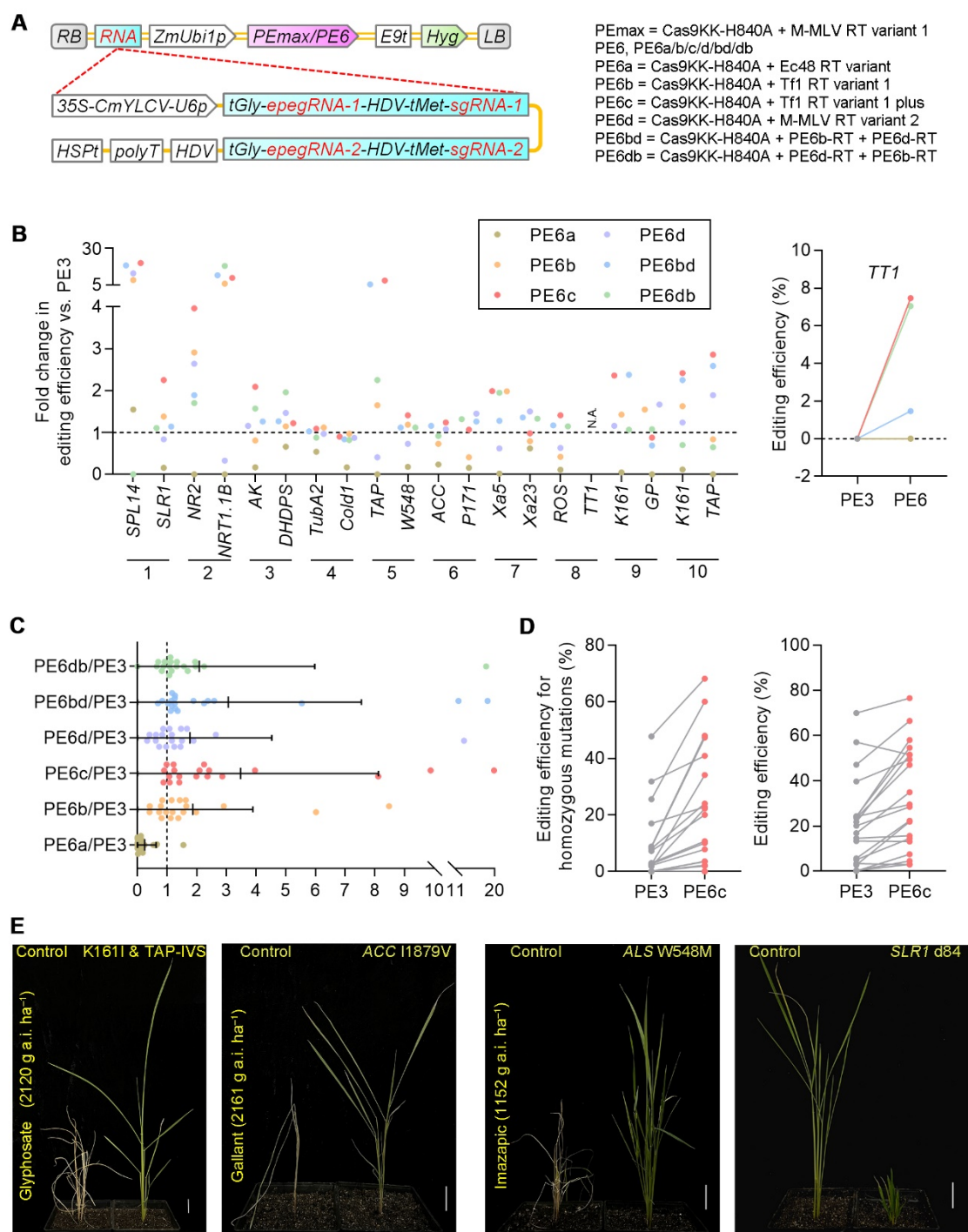


图1、PE6c大幅增强了水稻引导编辑。

Figure 1. PE6c greatly enhances prime editing in transgenic rice plants.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Cao Z[#], Sun W[#], Qiao D, Wang J, Li S, Liu X, Xin C, Lu Y, Gul S, Wang X, and Chen Q (2024) PE6c greatly enhances prime editing in transgenic rice plants. **J Integr Plant Biol** 66: 1864-1870.
2. Xin C, Qiao D, Wang J, Sun W, Cao Z, Lu Y, Jiang Y, Chai Y, Wang X, and Chen Q (2024) Enhanced editing efficiency in *Arabidopsis* with a LbCas12a variant harboring D156R and E795L mutations. **aBIOTECH** 5: 117-126.

专利授权:

1. 陈其军, 柴一萍, 姜媛媛; 一种提高先导编辑效率的载体和方法; 专利号: ZL202110812557.5; 授权公告日: 2024 年 04 月 16 日。
2. 陈其军, 姜媛媛, 柴一萍; 一种新型基因编辑系统及相关载体和方法; 专利号: ZL202110812232.7; 授权公告日: 2024 年 06 月 21 日。

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研究方向:挖掘玉米主要病害的抗性 QTL 基因；阐明寄主-病原互作的抗性机制；探究抗病 QTL 基因的分子进化路径；创制玉米抗病种质。

(一) 研究进展

1、玉米抗灰斑病基因 *ZmWAKL* 的克隆和抗病机理解析

玉米灰斑病是一种全球性的玉米病害，危害极其严重。在我国，玉米灰斑病已成为继玉米大斑病之后又一严重的叶部病害，一般减产 5-30%，发病严重时整株枯死，造成绝产。研究玉米抗灰斑病的遗传基础，挖掘优良等位变异位点，对培育抗灰斑病玉米品种、保障国家粮食安全具有重要意义。本研究通过图位克隆的方法鉴定到玉米抗灰斑病主效基因 *ZmWAKL*。*ZmWAKL* 编码一个细胞壁相关的类受体激酶，能够与共受体 *ZmWIK* 结合，增强彼此的磷酸化水平。*ZmWAKL/ZmWIK* 免疫复合体能够与细胞质受体激酶 *ZmBLK1* 结合并传递磷酸化信号。被激活的 *ZmBLK1* 能够直接结合并磷酸化 *ZmRBOH4*，从而正向调控玉米对灰斑病的抗性。研究表明 *ZmWAKL* 能够感知病原菌的入侵，并通过 *ZmWIK* 和 *ZmBLK1* 将免疫信号汇聚到 *ZmRBOH4*。激活的 *ZmRBOH4* 触发活性氧的爆发调控灰斑病抗性 (Zhong et al., *Nat Genet*, 2024)。

ZmWAKL-Mediated Immunity Underlies Quantitative Disease Resistance to Gray Leaf Spot in Maize

Gray leaf spot (GLS) is a destructive foliar disease and poses a grave threat to maize production worldwide. In China, GLS has become another serious foliar disease after Northern corn leaf blight, which causes 5-30% yield loss every year. When severely infected, the disease causes plant death, resulting in complete yield loss. It is of great significance to study the genetic basis of maize resistance to GLS and to mine the excellent allelic variation loci for breeding resistant varieties and ensuring national food security. We identified that *ZmWAKL* is causative gene underlying major QTL *qRgls1*. *ZmWAKL* encodes a cell wall-associated receptor-like kinase, which can bind to its co-receptor *ZmWIK* and enhance the phosphorylation level of each other. *ZmWAKL/ZmWIK* immune complex can bind to the receptor-like cytoplasmic kinase *ZmBLK1* and transmit phosphorylation signal. *ZmBLK1* directly binds and phosphorylates *ZmRBOH4*, thus positively regulating the GLS resistance. Our studies have shown that *ZmWAKL* could perceive the invasion of pathogen and converge immune signals to *ZmRBOH4* via *ZmWIK* and *ZmBLK1*. The activated *ZmRBOH4* finally triggers a burst of reactive oxygen species to execute GLS resistance



(Zhong et al., *Nat Genet*, 2024).

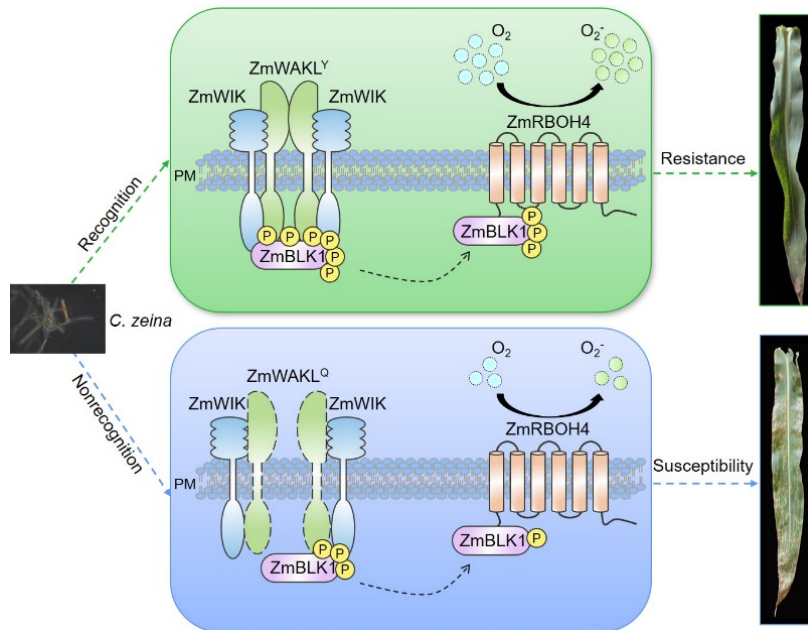


图 1、ZmWAKL 介导的玉米抗灰斑病工作模型。

Figure 1. Proposed working model for ZmWAKL-mediated GLS resistance in maize.

2、玉米广谱数量抗病基因 **ZmCPK39** 的克隆及分子机理解析

灰斑病、大斑病和小斑病是最为严重的玉米叶部病害。玉米对大斑病抗性可以分为小种特异的质量抗性和非小种特异的数量抗性，而对灰斑病和小斑病的抗性主要为数量抗性，且以加性效应为主。本研究通过图位克隆方法鉴定到同时对灰斑病、大斑病和小斑病具有广谱抗性的功能基因 **ZmCPK39**。病原菌诱导后，抗病等位基因 **ZmCPK39^{Y32}** 的表达水平显著低于感病等位基因 **ZmCPK39^{Q11}**。低丰度的 **ZmCPK39^{Y32}** 导致下游转录因子 **ZmDi19** 磷酸化程度降低，蛋白降解减少。富集的 **ZmDi19** 能够结合病情相关蛋白编码基因 **ZmPR10** 的启动子并正调控其表达，从而赋予玉米对灰斑病、大斑病和小斑病的抗性 (Zhu et al., *Nat Genet*, 2024)。

A Calcium-Dependent Protein Kinase Regulates Broad-Spectrum Quantitative Resistance to Multiple Foliar Diseases in Maize

Gray leaf spot (GLS), Northern leaf blight (NLB), and Southern leaf blight (SLB) are three of the most destructive foliar diseases in maize. Resistance to NLB is controlled by both race-specific major effect (qualitative) genes and by non-race quantitative trait loci (QTL) with minor effects. All known maize resistance to both GLS and SLB is controlled by QTL, most with small or moderate additive effects. Here, we identified that **ZmCPK39**, a calcium-dependent protein kinase, mediates broad-spectrum quantitative resistance to GLS, NLB, and SLB in maize. We showed that pathogens induced expression level of resistant allele **ZmCPK39^{Y32}** was significantly lower than

susceptible allele *ZmCPK39*^{Q11}. The relative lower abundance of *ZmCPK39*^{Y32} leads to reduced phosphorylation and degradation of the transcription factor *ZmDi19*. The high *ZmDi19* abundance in turn causes higher *ZmPR10* expression, enhancing maize resistance to GLS, NLB, and SLB (Zhu et al., *Nat Genet*, 2024).

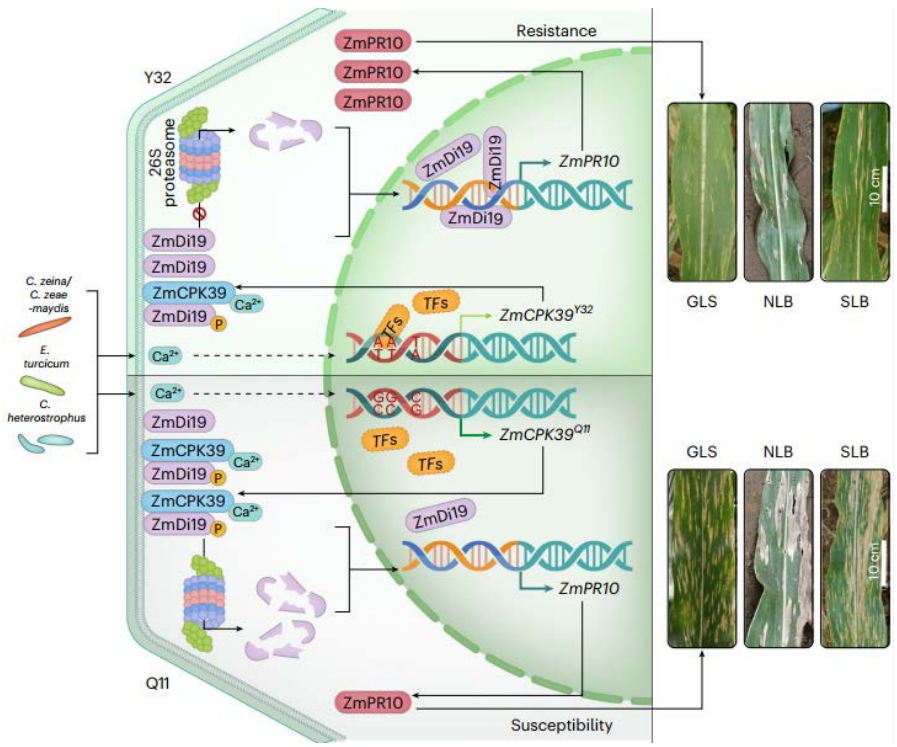


图 2、*ZmCPK39* 介导的玉米广谱数量抗病工作模型。
Figure 2. Proposed working model of *ZmCPK39*-mediated maize resistance to GLS, NLB, and SLB.

3、*ZmGDla-hel* 调控玉米粗缩病隐性数量抗性的机理解析

粗缩病是一种分布广泛的病毒性病害，俗称玉米“癌症”。前期研究中，作者通过图位克隆的方法鉴定了 *helitron* 转座子插入感病基因 *ZmGDla* 的突变体(*ZmGDla-hel*)是玉米粗缩病的隐性数量抗性基因。进一步研究揭示，病毒致病因子 P7-1 通过靶向结合感病因子 *ZmGDla* 引起发病，而 P7-1 因结合抗病蛋白 *ZmGDla-hel* 的能力减弱，最终导致隐性数量抗性。作者发现了另一个关键的寄主蛋白—赤霉素氧化酶 13(*ZmGA2ox7.3*)，其与感病蛋白 *ZmGDla* 和病毒致病因子 P7-1 的结合能力显著强于抗病蛋白 *ZmGDla-hel*，是粗缩病发生的重要参与者。研究表明，*ZmGA2ox7.3* 在其自身多聚化后，酶活性显著增强，能够迅速将生物活性的赤霉素及其前体转化为无活性的形式。在 RBSDV 侵染感病材料(携带 *ZmGDla* 基因)后，P7-1/*ZmGDla* 复合物显著诱导 *ZmGA2ox7.3* 的表达，促进 P7-1/*ZmGDla* 与 *ZmGA2ox7.3* 之间多聚化的形成，进一步增强 *ZmGA2ox7.3* 的酶活性。其结果导致生物活性赤霉素减少，继而破坏生长素/细胞分裂素的平衡，最终引发节间缩短的玉米粗缩病症状。相反，在抗性材料(携带 *ZmGDla-hel* 基因)中，P7-1 与 *ZmGDla-hel* 的相互作用减弱，几乎不诱导 *ZmGA2ox7.3* 的表达，因此对病毒诱发的生物活性赤霉素减少和激素不平衡的影响较小，从而降低



粗缩病发病的严重程度，表现出隐性数量抗性 (Deng et al., *Nat. Commun*, 2024)。

Molecular Mechanisms of ZmGDI α -hel in Regulating Maize Quantitative Recessive Resistance to MRDD

Maize rough dwarf disease (MRDD) is a predominant viral disease, commonly referred to as ‘the cancer of maize’. Our previous study showed that a *helitron*-induced *ZmGDI α* variant is the recessive resistant gene, leading to quantitative resistance to MRDD. The P7-1 effector of the rice black-streaked dwarf virus (RBSDV) targets maize Rab GDP dissociation inhibitor α (ZmGDI α) to cause MRDD. However, P7-1 has difficulty recruiting a ZmGDI α variant with an alternative *helitron*-derived exon 10 (ZmGDI α -hel), resulting in recessive resistance. Here, we demonstrate that P7-1 can recruit another maize protein, gibberellin 2-oxidase 13 (ZmGA2ox7.3), which also exhibits tighter binding affinity for ZmGDI α than ZmGDI α -hel. The oligomerization of ZmGA2ox7.3 is vital for its function in converting bioactive gibberellins into inactive forms. Moreover, the enzymatic activity of ZmGA2ox7.3 oligomers increases when forming hetero-oligomers with P7-1/ZmGDI α , but decreases when ZmGDI α -hel replaces ZmGDI α . Viral infection significantly promotes *ZmGA2ox7.3* expression and oligomerization in ZmGDI α -containing susceptible maize, resulting in reduced bioactive GA₁/GA₄ levels. This causes an auxin/cytokinin imbalance and ultimately manifests as MRDD syndrome. In contrast, in resistant plants (carrying the *ZmGDI α -hel* gene), the interaction between P7-1 and *ZmGDI α -hel* is weakened, leading to minimal induction of *ZmGA2ox7.3* expression. Consequently, the virus-induced reduction in bioactive gibberellins and hormonal imbalance are mitigated, reducing the severity of MRDD and manifesting as recessive quantitative resistance (Deng et al., *Nat Commun*, 2024).

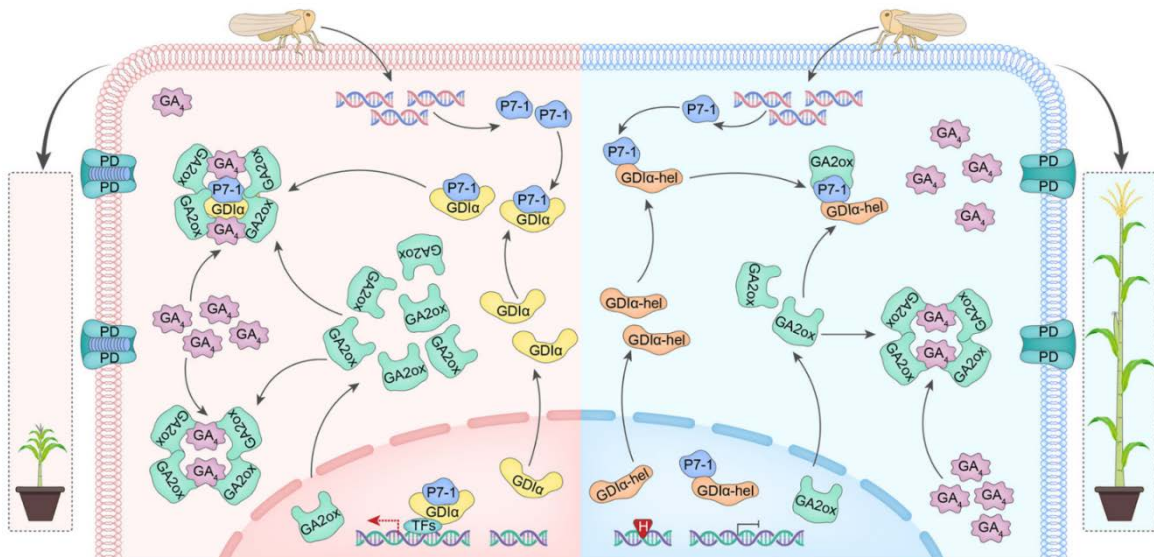


图 3、粗缩病病症发展的模式图。

Figure 3. A working model for the development of MRDD symptoms.



4、玉米抗丝黑穗病蛋白 ZmWAK 介导的分子模块解析

玉米丝黑穗病是活体真菌 *Sporisorium reilianum* 引起的土传性病害。前期研究证实，主效抗病基因是 *ZmWAK*，它编码细胞壁相关蛋白激酶，位于细胞膜。本研究发现 *ZmWAK* 蛋白激酶活性受丝轴黑粉菌侵染诱导，在短时间内显著提高，而后触发 *ZmWAK* 对 *ZmSnRK1α2* 的互作和磷酸化，促使 *ZmSnRK1α2* 从细胞质转移到细胞核中。细胞核中的 *ZmSnRK1α2* 会磷酸化并降低转录因子 *ZmWRKY53* 稳定性。*ZmWRKY53* 负调控玉米丝黑穗病抗性。组学结果表明 *ZmWRKY53* 降解时，编码跨细胞膜转运的 *SWEETs*、水通道等蛋白的基因表达量降低，导致向膜外转运的营养物质减少，如糖类、氨基酸、水分和离子等。这一改变导致质外体营养物质匮乏，限制病原菌生长，表现抗病。(Zhang et al., *Mol Plant*, 2024)。

A Maize WAK-Snrk1α2-WRKY Module Regulates Nutrient Availability to Defend Against Head Smut Disease

Maize head smut, a devastating soil-borne disease, is caused by the fungal pathogen *Sporisorium reilianum*. Previous studies indicated that the *ZmWAK* gene, encoding a cell wall-associated kinase, confers quantitative disease resistance (QDR) against head smut. *ZmWAK*, a receptor kinase localized to the plasma membrane, is activated by specific, yet unidentified, signatures from *S. reilianum*, leading to the recruitment and subsequent phosphorylation of the cytoplasmic *ZmSnRK1α2*. Once phosphorylated, *ZmSnRK1α2* relocates from the cytoplasm to the nucleus, where it affects the stability of the negative regulator *ZmWRKY53*. The degradation of *ZmWRKY53* then prompts the downregulation of transmembrane transport genes. Consequently, this chain of events results in reduced nutrient availability, thereby curtailing the colonization of *S. reilianum* in the apoplast (Zhang et al., *Mol Plant*, 2024).

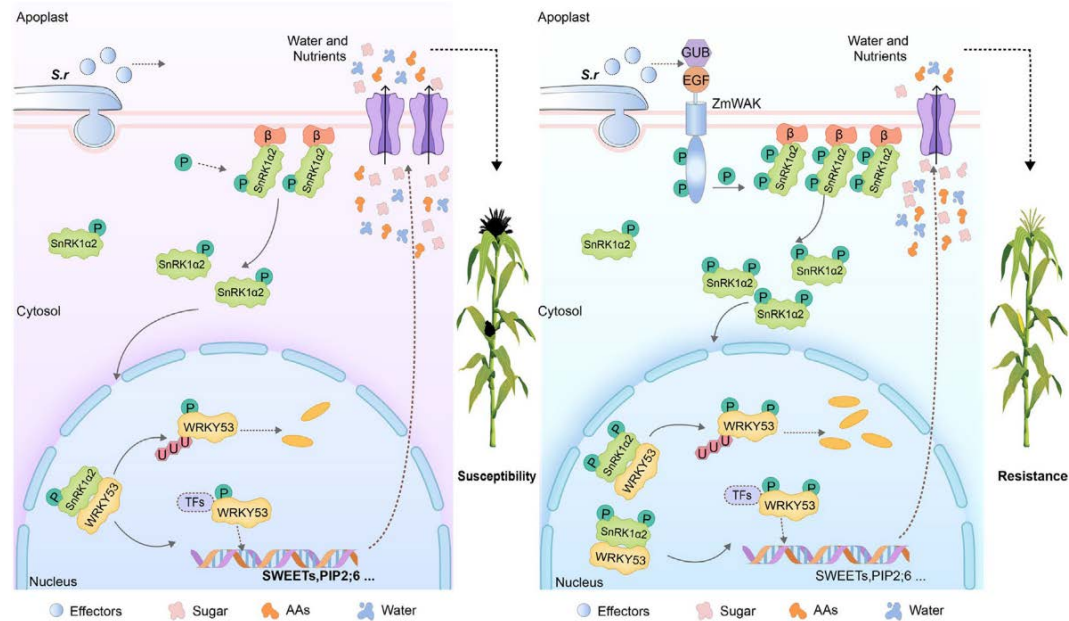


图4、抗病蛋白ZmWAK介导玉米丝黑穗病抗性的分子模型。

Figure 4.The proposed working model for ZmWAK-mediated molecular module for resistance to head smut in maize.



5、玉米抗茎腐病基因的挖掘和应用

茎腐病是世界各玉米产区普遍发生的重要土传性病害，在乳熟期造成根茎基部腐烂，叶片青枯，籽粒灌浆受阻，到收获期，造成大面积倒伏，影响产量和品质。茎腐病近年来在我国各玉米产区普遍发生，减产 25~30%，甚至绝收，危害极其严重。

玉米抗茎腐病新位点功能基因的克隆：在本研究中，我们对接近免疫茎腐病的玉米自交系 CML304 进行了全基因组测序和从头组装。通过 CML304 和 B73 组配的 BC₂F₅ 群体进行 QTL 定位，鉴定出一个来源于 CML304 的抗性位点 *qRfg4*。精细定位将 QTL-*qRfg4* 缩小到 900kb 的物理区间。遗传效应估计 QTL-*qRfg4* 能够显著降低病情指数(DSI)17.8%。

主效抗病 QTL 基因 *ZmCCT* 的基因编辑和育种应用：*ZmCCT* 是一个主效的抗茎腐病基因，同时在长日照条件下延迟开花。前期研究将抗病 *ZmCCT* 单倍型 H6 导入到玉米骨干自交系郑 58 和昌 7-2 中，田间表型鉴定发现在郑 58 和昌 7-2 背景下，导入 H6 的材料茎腐病抗性显著提高的同时表现出了强烈的光周期敏感性，显著延迟开花期。因此利用 CRISPR/Cas9 技术，对 *ZmCCT* 抗病单倍型 H6 启动子区响应光周期的 5 个靶标区域进行编辑，经过筛选在郑 58 和昌 7-2 两个背景中共获得有代表性的 45 种编辑材料进行表型鉴定。本年度鉴定了 BC₃F₃ 代分离群体 *ZmCCT* 启动子区编辑材料在长日照条件下的开花期和茎腐病抗性。通过表型鉴定，我们确定编辑类型 d1+d1 材料综合表现较好，在抗茎腐病的同时开花期没有显著推迟，且在两年间性状表现稳定。

Identification and Utilization of Genes Against Stalk Rot Disease in Maize

Maize stalk rot is one of the most devastating and prevalent diseases worldwide. In the grain-filling stage, the disease causes rhizome rot, leaves yellowing and grain-filling block. At the harvest stage, stalk rot disease leads to large-scale plant lodging, which causes yield loss and deterioration of grain quality. In recent years, stalk rot has widely spread in all maize producing areas in China, with a yield reduction of 25-30%, or even complete yield loss.

Cloning of causative gene underlying a new resistance locus against maize *Gibberella* stalk rot: In this study, we performed whole-genome sequencing and *de novo* assembly of the nearly immune inbred line CML304. Using a BC₂F₅ population derived from a cross between CML304 and B73, we performed QTL mapping analysis and identified a resistance locus, *qRfg4*, inherited from CML304. Fine mapping narrowed the QTL-*qRfg4* to a 900 kb physical region. Genetic effect analysis estimated that QTL-*qRfg4* could significantly reduce the disease severity index (DSI) by 17.8%.

The modification and application of a stalk rot resistance gene *ZmCCT*: *ZmCCT* is the gene underlying the major resistance QTL against stalk rot, which can also delay maize flowering time under long-day conditions. In our previous study, the H6 haplotype of *ZmCCT* were introduced into elite maize inbred lines Zheng58 and Chang7-2. We analyzed the stalk rot resistance and photoperiod sensitivity, the resistance H6 haplotype has photoperiod sensitivity under long-day conditions. To eliminate the bad attribute, we used CRISPR/Cas9 to edit the promoter sequence



which contain photoperiod responsiveness cis-elements. After selected, we got 45 types of editing materials to evaluate the disease resistance and photoperiod sensitivity. Phenotypic identification results showed that d1+d1 showed desirable phenotypes, which can early flowering and remain unchangeable disease resistance.

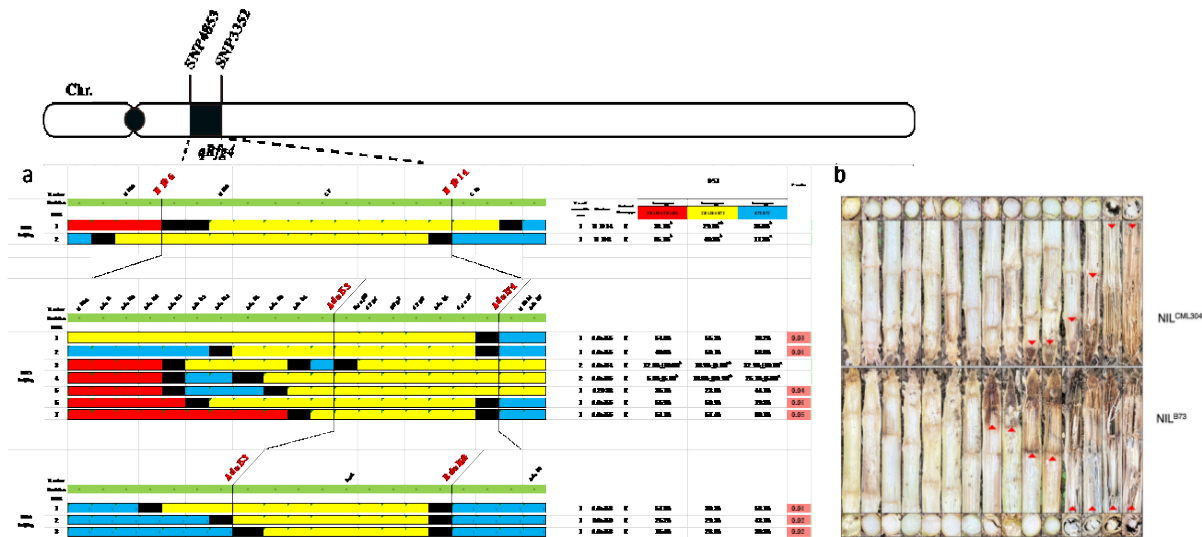


图 5、QTL-*qRfg4* 精细定位。
Figure 5. Fine Mapping of QTL-*qRfg4*.

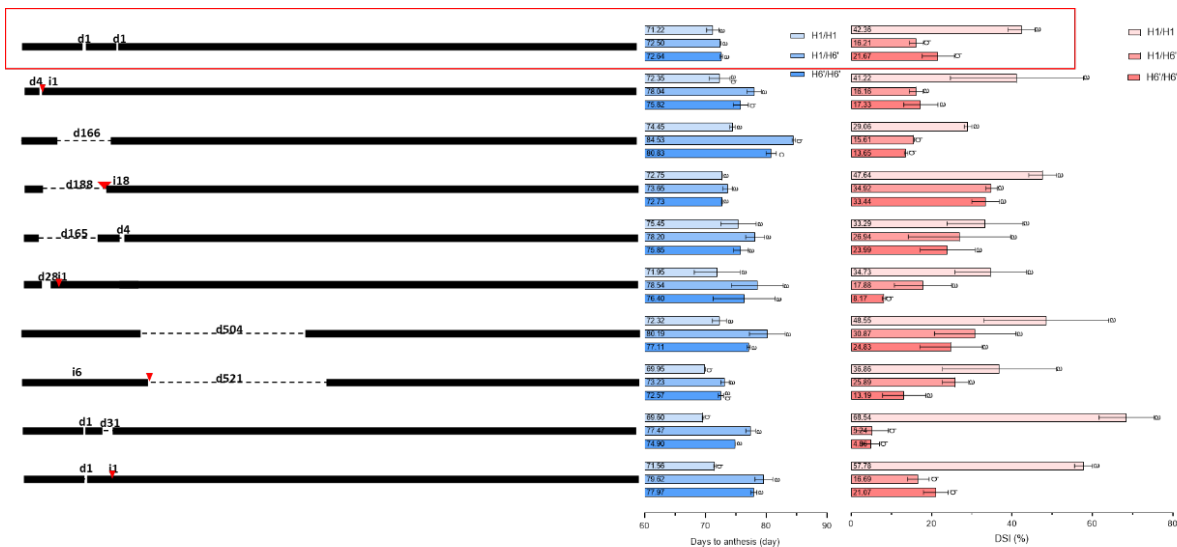


图 6、昌 7-2 背景分离编辑材料开花期和抗病性表型分析。
Figure 6. The flowering time assessment and disease resistance evaluation of segregation population of edited plants in Chang7-2 background.

6、玉米抗拟轮枝镰孢菌穗腐病 QTL 的精细定位

玉米穗粒腐病是世界范围内发生的危害严重的真菌性病害，不仅造成玉米产量的下降，产生的真菌毒素还对人畜的健康构成严重的威胁。近年来，随着气候的变化，玉米穗粒腐病已蔓延成为玉



米种植区最严重的病害，成为育种家最关心的问题。我们利用 RIL 群体在 2 号染色体上定位到一个穗腐病抗性位点 QTL-*qRfv2*，经过多次精细定位将区间最终锁定到 1.01Mb 区间内。根据 B73 参考基因组，该区间内有 60 个基因，其中 28 个基因有功能注释。

结合亲本转录组数据，发现有 22 个基因在接种或非接种时有表达。比较接种后双亲之间的差异表达基因，发现有 7 个基因(*ZmLOX6*, *ZmCSN5B*, *ZmNADPH*, *ZmWAKL10*, *ZmTAD1*, *ZmRRP1B*, *ZmAAP16*)在每个时间点都有差异，其中 *ZmLOX6*, *ZmCSN5B* 和 *ZmNADPH* 表达量较高。比较同一材料里接种和非接种之间的差异表达基因，发现抗病材料里接种 4 小时后，*ZmPPKSP* 和 *ZmRRP1B* 差异表达。而在感病材料里，*ZmIBH1* 和 *ZmWAKL10* 在 1 小时达到差异，而 *ZmMHA2* 和 *ZmPPKSP* 在 4 小时才有差异。表明这些基因可能在抵御病原体入侵时发挥作用 (图 7)。

Fine-Mapping of Resistance QTL to *Fusarium* Ear Rot in Maize

Maize ear rot, one of the most devastating fungal diseases worldwide, not only reduces maize yield but also poses severe health risks to humans and livestock due to mycotoxins produced by *Fusarium* spp. With recent climate changes, maize ear rot has spread to all maize-growing areas, becoming the most serious disease and a primary concern for maize breeders. We used the recombinant inbred lines (RIL) population to identify resistance genes against *Fusarium verticillioides* ear rot in maize. The major QTL-*qRfv2* was identified on chromosome 2, and its region was narrowed to 1.01Mb after several rounds of fine-mapping. According to the B73 reference genome, there are about 60 genes in this region, 28 of which have functional annotations.

Through RNA-seq analysis, we found that 22 of the 28 functional genes were expressed under either inoculated or non-inoculated conditions. After comparing DEGs between B73 and CML304 at various time points post-inoculation, it was observed that certain genes exhibited variations at each time point, namely *ZmLOX6*, *ZmCSN5B*, *ZmNADPH*, *ZmWAKL10*, *ZmTAD1*, *ZmRRP1B* (ID: and *ZmAAP16*. Among these, *ZmLOX6*, *ZmCSN5B*, and *ZmNADPH* exhibited higher FPKM values. Additionally, we analyzed DEGs between inoculated and non-inoculated samples from the same line. *ZmPPKSP* and *ZmRRP1B* exhibited significant differences within the resistant line 4 hours post inoculation. Meanwhile, in the susceptible line B73, *ZmIBH1* and *ZmWAKL10* genes showed differential expression at 1 hpi, and *ZmMHA2* and *ZmPPKSP* at 4 hpi. This suggests that these genes may play a role in the defense against pathogens (Figure7).

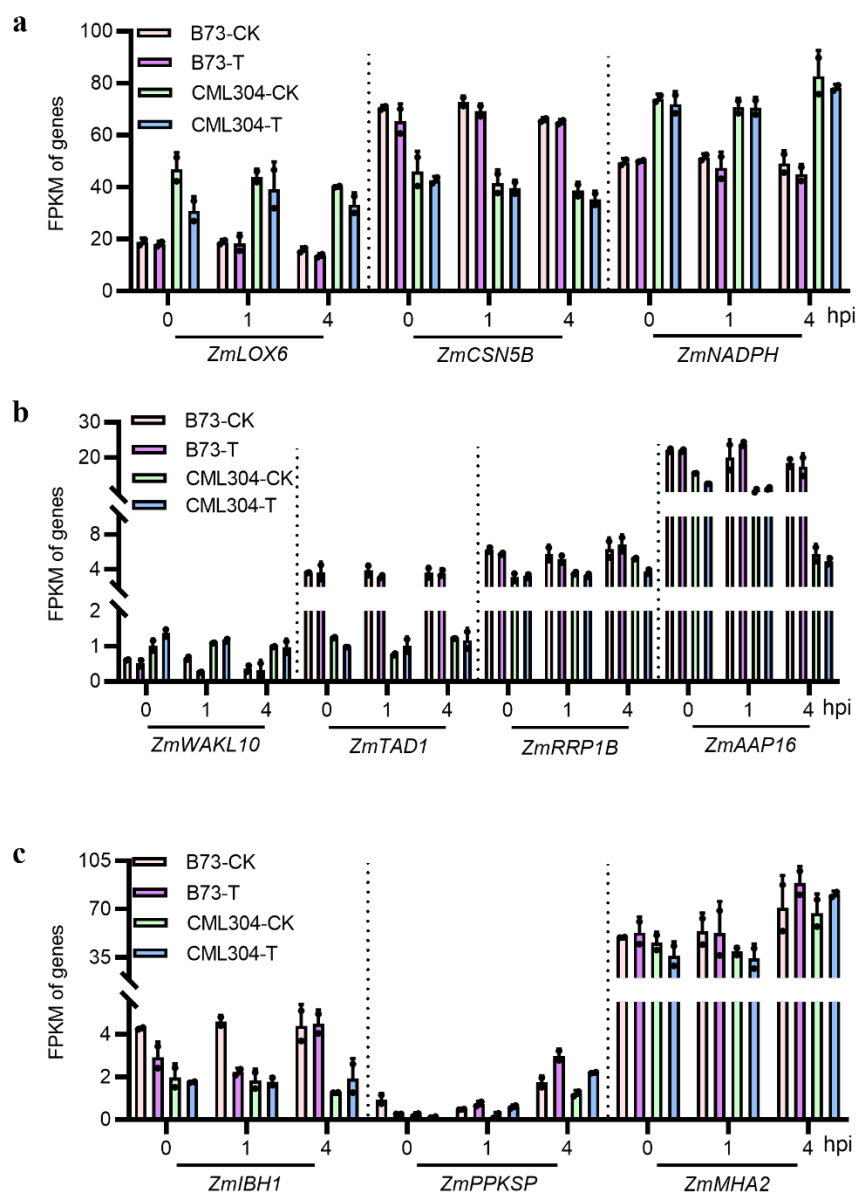


图 7、候选基因诱导表达分析。
Figure 7. The FPKM of candidate genes in B73 and CML304 after inoculation or non-inoculated conditions.

7、玉米籽粒含水量基因的挖掘和应用

实现玉米生产全程机械化对于确保国家粮食安全、促进产业兴农有重要意义。收获期籽粒含水量过高是限制玉米籽粒直收的主要因素。目前我国玉米籽粒直收占比不足 5%，其原因主要是大多数推广品种收获期含水量在 30%以上，高于粒收标准(GWC<25%)。由于我国多数种植区域实施麦玉两季轮作制，加快籽粒脱水能够缩短玉米种植周期、节约人力成本、提高籽粒品质。此外，降低籽粒含水量还能够减少玉米穗腐病和籽粒霉变的发生。挖掘并聚合低 GWC 或脱水快基因进行遗传改良，降低现有生产品种 GWC，将有助于加快实现机械化收获。



玉米籽粒含水量 QTL-*qGwc1* 的机理研究: 本年度主要做了以下内容。针对 *qGwc1* 培育了一对近等基因系: NIL^H (高 GWC)和 NIL^L (低 GWC)。与 NIL^H 相比, NIL^L 的籽粒水重(GWW)和鲜籽粒体积减少, 但不影响干物质积累。在籽粒发育后期(授粉后 35 天), NIL^L 比 NIL^H 的籽粒脱水速率更快, 使得两者之间的 GWC 差异进一步扩大。激素测定表明, NIL^L 早期籽粒中 JA 含量显著减少, 而细胞分裂素, 生长素的储藏态(IAA-Glu 和 IAA-ASP)和前体(IPA)等含量显著增加(Liu et al., *Crop J*, 2024)。

玉米籽粒含水量 QTL-*qGwc2* 的挖掘: 本年度对前期鉴定到 QTL-*qGwc1.2*, 通过加密分子标记开展精细定位。2023 年冬, 利用 19 个重组个体的 1697 株后代开展精细定位工作, 将 *qGwc1.2* 定位到分子标记 K452 和 K453 之间约 450bp 的区间内。2024 年夏, 利用 17 个重组个体的 1801 株后代所开展的精细定位工作验证了 2023 年冬的精细定位结果。通过比对 B73 V5 版本参考序列, 以及双亲 *de novo* 测序数据进行基因预测, 最终确定定位区段位于基因 *ZmCYP* 上游调控区。

Fine-Mapping of QTL for Grain Water Content in Maize

The mechanization of maize production plays a pivotal role in global food security and agricultural advancement. However, in China and many other countries, maize harvesting remains largely unmechanized, with less than 5% of grain harvested mechanically in China. This is primarily due to the high grain water content (GWC), which typically exceeds 30% at harvest (Li et al., 2018), surpassing the recommended threshold of 25% suitable for mechanical harvesting. High GWC prolongs the growing season, raises costs, and reduces grain quality. Moreover, ears with high GWC are particularly vulnerable to ear/grain rot in the field and mildew during storage and transportation. Consequently, reducing GWC has emerged as a central focus in maize breeding, with efforts centered on identifying and incorporating genetic factors associated with low GWC or fast grain dehydration rate (GDR) into current maize varieties to enable efficient mechanized harvesting.

Molecular mechanism of QTL-*qGwc1* for grain water content in maize: The main things we did during the year were as follows. Here, we examined two near-isogenic lines (NILs), NIL^L and NIL^H , differing at the *qGWC1* locus, and observed that the lower GWC in NIL^L is primarily attributed to reduced grain water weight (GWW) and smaller fresh grain size, rather than the accumulation of grain dry matter. Notably, the difference in GWC between the two NILs became more pronounced approximately 35 days after pollination (DAP), arising from a faster dehydration rate in NIL^L . Through an examination of hormones and their derivatives, we detected a marked decrease in jasmonic acid (JA), alongside a notable increase in cytokinin, storage forms of IAA (IAA-Glu, IAA-ASP), and the IAA precursor IPA in immature NIL^L kernels (Liu et al., *Crop J*, 2024).

Mining of QTL-*qGwc2* of maize grain water content: For previously identified QTL-*qGwc1.2*, we developed molecular markers in the localization interval for further fine-mapping. In Hainan Winter Nursery, the 1697 offspring of 19 recombinant individuals were used to fine mapping

the QTL- *qGwc1.2*. And the *qGwc1.2* was fine-mapped to a 450bp interval between markers K452 and K453. The fine mapping results obtained in Hainan was validated by additional fine mapping work in Shandong using 17 recombined individuals' 1801 offspring. By comparing to the B73 V5 reference sequence and the gene prediction of *de novo* sequencing data from the parents, the *qGwc1.2* was determined to be located in the upstream regulatory region of the *ZmCYP* gene.

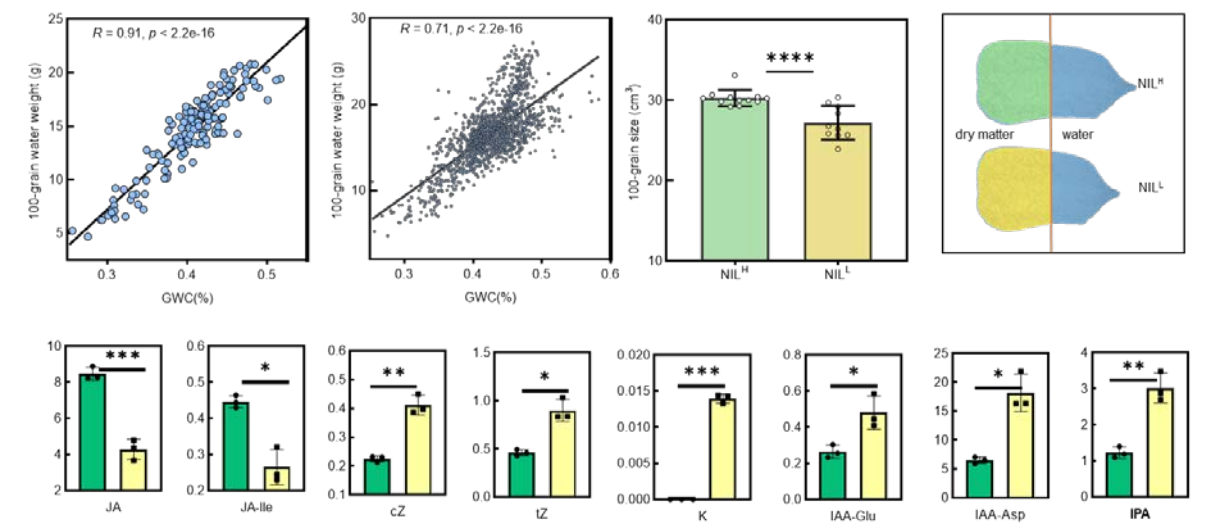


图 8、*qGwc1* 调控籽粒含水量的机制解析。
Figure 8. Mechanisms of *qGwc1* regulation of GWC.

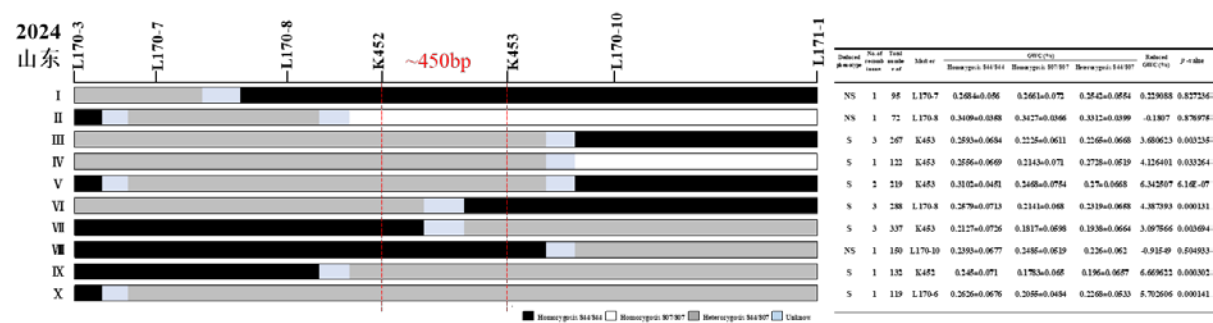


图 9、*qGwc1.2* 精细定位。
Figure 9. Fine mapping of *qGwc1.2*.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

- Zhong T, Zhu M, Zhang Q, Zhang Y, Deng S, Guo C, Xu L, Liu T, Li Y, Bi Y, Fan X, Balint-Kurti P, Xu M* (2024) ZmWAKL-mediated immunity underlies quantitative disease resistance to gray leaf spot in maize. *Nat Genet* 56: 315-326.
- Zhu M, Zhong T, Xu L, Guo C, Zhang X, Liu Y, Zhang Y, Li Y, Xie Z, Liu T, Jiang F, Fan X, Balint-Kurti P, Xu M* (2024) The ZmCPK39-ZmDi19-ZmPR10 immune module regulates



- quantitative resistance to multiple foliar diseases in maize. *Nat Genet* 56: 2815–2826.
3. Deng S, Jiang S, Liu B, Zhong T, Liu Q, Liu J, Liu Y, Yin C, Sun C, Xu M* (2024) ZmGDI α -hel counters the RBSDV-induced reduction of active gibberellins to alleviate maize rough dwarf virus disease. *Nat Commun* 15:7576.
 4. Zhang Q, Xu Q, Zhang N, Zhong T, Xing Y, Fan Z, Yan M, Xu M* (2024) A maize WAK-SnRK1 α 2-WRKY module regulates nutrient availability to defend against head smut disease. *Mol Plant* 17(11):1654-1671.
 5. Zhu M, Guo C, Zhang X, Liu Y, Jiang X, Chen L, Xu M* (2024) The maize ZmCPK39-ZmKnox2 module regulates plant height. *ABIOTECH* 5:356-361.
 6. Liu Y, Li M, Liu J, Deng S, Zhang Y, Xia X, Liu B, Xu M* (2024) Multi-omics analysis reveals the pivotal role of phytohormone homeostasis in regulating maize grain water content. *Crop J* 12:1081-1092.

专利授权

1. 徐明良, 钟涛, 朱芒, 郭晨煜, 房正, 张晓辉; 玉米灰斑病抗性相关蛋白及其编码基因与应用; 专利号: ZL 2022 1 0012417.4, 授权公告日: 2024 年 02 月 20 日。
2. 徐明良, 钟涛, 番兴明, 朱芒, 张艳, 徐凌, 刘丽; 灰斑病抗性相关蛋白 ZmWAK-RLK 及其编码基因和应用; 专利号: ZL 2020 8 0013982.1, 授权公告日: 2024 年 03 月 26 日。
3. Mingliang Xu, Tao Zhong, Xingming Fan, Mang Zhu, Yan Zhang, Ling Xu, Li Liu; ZmWAK-RLK protein related to gray leaf spot resistance, and encoding gene and application thereof; 专利号: US 12,077,769 B2, 授权公告日: 2024 年 09 月 03 日。

(三) 研究队伍

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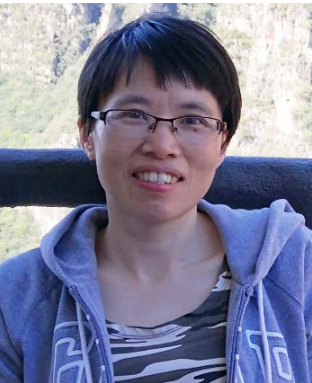
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研究方向：玉米产量品质性状的遗传基础与分子育种。

(一) 研究进展

利用多亲群体的连锁分析和关联分析解析玉米籽粒类胡萝卜素的遗传基础

类胡萝卜素不仅对植物的生长发育至关重要，还是人类膳食中的关键营养成分。尽管类胡萝卜素代谢途径在植物中高度保守，但对于多数谷物作物，对其种子类胡萝卜素变异的遗传基础仍缺乏深入了解。本研究以六个重组自交系(RIL)群体为材料，对八个类胡萝卜素相关性状进行系统的连锁分析和关联分析。单群体连锁分析(SLM)和联合连锁分析(JLM)共鉴定到 77 个加性 QTL 和 104 对上位性 QTL，其中 22 个位点为加性 QTL 和上位性 QTL 的共有热点，表明部分 QTL 可以通过加性或上位性机制调控玉米籽粒类胡萝卜素的变异。此外，基于 RIL 群体的全基因组关联分析(GWAS)鉴定到 244 个与类胡萝卜素相关性状显著关联的候选基因，其中 23 个被注释为类胡萝卜素代谢途径的关键酶基因。对候选基因所在关联位点的遗传效应进行比较发现，尽管少数类胡萝卜素代谢途径关键酶基因的自然变异能够解释更大的表型变异，但大量非代谢途径的基因/位点在类胡萝卜素的变异中也起着重要作用。在此基础之上，我们在二号染色体上鉴定到一个加性/上位性热点 Q10/JLM10/GWAS019，通过精细定位和基因编辑克隆了该 QTL 的功能基因 *ZmPTOX*。*ZmPTOX* 编码质体末端氧化酶，其催化产物质体醌是类胡萝卜素合成途径关键酶 PDS 和 ZDS 的辅助因子。候选基因关联分析发现，位于启动子和第二外显子上的自然变异可能是 *ZmPTOX* 影响类胡萝卜素变异的功能位点。该研究系统地解析了玉米类籽粒胡萝卜素变异的遗传机制，为类胡萝卜素代谢工程的重塑及其高效的生物强化提供理论依据和新的靶标基因。相关结果以封面文章发表在 *Plant Biotechnol J* 期刊上 (Yin et al., *Plant Biotechnol J*, 2024)。

Linkage and Association Mapping in Multi-Parental Populations Reveal the Genetic Basis of Carotenoid Variation in Maize Kernels

Carotenoids are indispensable to plants and critical components of the human diet. The carotenoid metabolic pathway is conserved across plant species, but our understanding of the genetic basis of carotenoid variation remains limited for the seeds of most cereal crops. To address this issue, we systematically performed linkage and association mapping for eight carotenoid traits using six recombinant inbred line (RIL) populations. Single linkage mapping (SLM) and joint linkage



mapping (JLM) identified 77 unique additive QTLs and 104 pairs of epistatic QTLs. Among these QTLs, we identified 22 overlapping hotspots of additive and epistatic loci, highlighting the important contributions of some QTLs to carotenoid levels through additive or epistatic mechanisms. A genome-wide association study based on all RILs detected 244 candidate genes significantly associated with carotenoid traits, 23 of which were annotated as carotenoid pathway genes. Effect comparisons suggested that a small number of loci linked to pathway genes have substantial effects on carotenoid variation in our tested populations, but many loci not associated with pathway genes also make important contributions to carotenoid variation. We identified *ZmPTOX* as the causal gene for a QTL hotspot (*Q10/JLM10/GWAS019*); this gene encodes a putative plastid terminal oxidase that produces plastoquinone-9 used by two enzymes in the carotenoid pathway. Natural variants in the promoter and second exon of *ZmPTOX* were found to alter carotenoid levels. This comprehensive assessment of the genetic mechanisms underlying carotenoid variation establishes a foundation for rewiring carotenoid metabolism and accumulation for efficient carotenoid biofortification (Yin et al., *Plant Biotechnol J*, 2024).

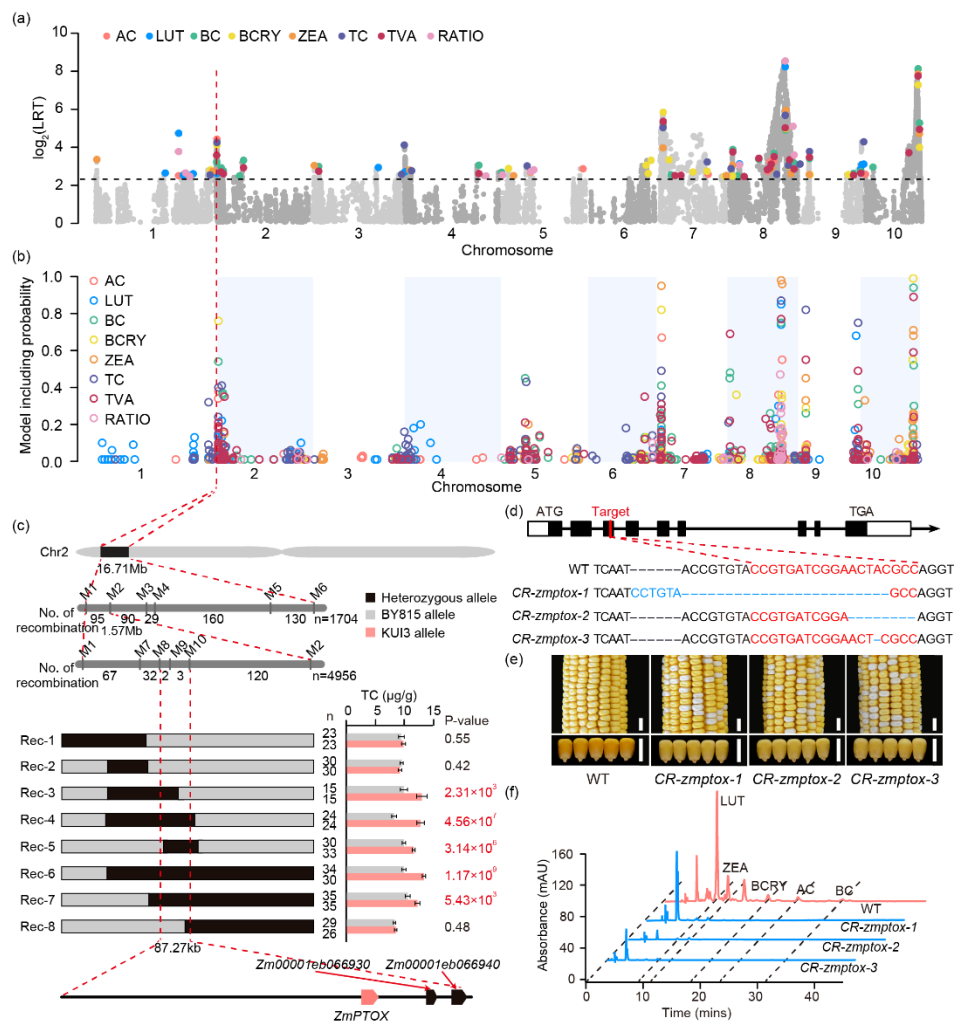


图1、玉米籽粒类胡萝卜素的遗传基础和*ZmPTOX*的克隆与功能验证。

Figure 1. Genetic basis of carotenoids in maize kernels and cloning and functional validation of *ZmPTOX*.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Yin P[#], Fu X[#], Feng H[#], Yang Y[#], Xu J, Zhang X, Wang M, Ji S, Zhao B, Fang H, Du X, Li Y, Hu S, Li K, Xu S, Li Z, Liu F, Xiao Y, Wang Y, Li J, Yang X* (2024) Linkage and association mapping in multi-parental populations reveal the genetic basis of carotenoid variation in maize kernels. **Plant Biotechnol J** 22(8): 2312-2326.

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田丰，教授。国家杰出青年科学基金获得者（2020），国家优秀青年科学基金获得者（2013），青年创新人才项目（2012），获得中国“科学探索奖”（2024）。

研究方向：玉米驯化与适应的分子遗传机制。

（一）研究进展

1、智慧株型基因促进玉米密植增产

增加种植密度是提高玉米产量的关键措施，“上部叶片紧凑、中下部叶片相对松散”的智慧株型能够最大限度捕获光能，获得更高的群体产量。田丰和李继刚课题组合作首次发现玉米中智慧株型基因 *lac1*，该基因编码一个 BR 信号途径合成酶，能够调控玉米植株提高群体光合能力，减弱密植群体避荫反应。本研究揭示了光受体 *phyA* 与叶夹角关键调控因子 *ZmRAVL1* 互作，利用 26S 蛋白酶降解途径动态调控 *lac1* 促进玉米适应密植的调控机制。多年多点的田间产量试验表明 *lac1* 能够显著提高玉米密植群体产量。研究人员开发了融合诱导系和基因编辑的技术体系，通过 20 个纯合 DH 系重现了智慧株型的表型特征，预演了该技术快速、高效创制玉米种质资源的广阔应用前景。总之，本研究不仅为玉米智慧株型顶层设计提供了理论基础和关键基因资源；同时，开发的先进技术体系实现了分子设计育种从理论研究到应用场景的衔接。

Maize Smart-Canopy Architecture Enhances Yield at High Densities

Increasing planting density is a key strategy for enhancing maize yields. An ideotype for dense planting requires a 'smart canopy' with leaf angles at different canopy layers differentially optimized to maximize light interception and photosynthesis, among other features. Here we identified *leaf angle architecture of smart canopy 1 (lac1)*, a natural mutant with upright upper leaves, less erect middle leaves and relatively flat lower leaves. *lac1* has improved photosynthetic capacity and attenuated responses to shade under dense planting. *lac1* encodes a brassinosteroid C-22 hydroxylase that predominantly regulates upper leaf angle. Phytochrome A photoreceptors accumulate in shade and interact with the transcription factor RAVL1 to promote its degradation via the 26S proteasome, thereby inhibiting activation of *lac1* by RAVL1 and decreasing brassinosteroid levels. This ultimately decreases upper leaf angle in dense fields. Large-scale field trials demonstrate that *lac1* boosts maize yields under high planting densities. To quickly introduce *lac1* into breeding germplasm, we transformed a haploid inducer and recovered homozygous *lac1* edits from 20 diverse inbred lines. The tested doubled haploids uniformly acquired smart-canopy-like



plant architecture. We provide an important target and an accelerated strategy for developing high-density-tolerant cultivars, with *lac1* serving as a genetic chassis for further engineering of a smart canopy in maize.

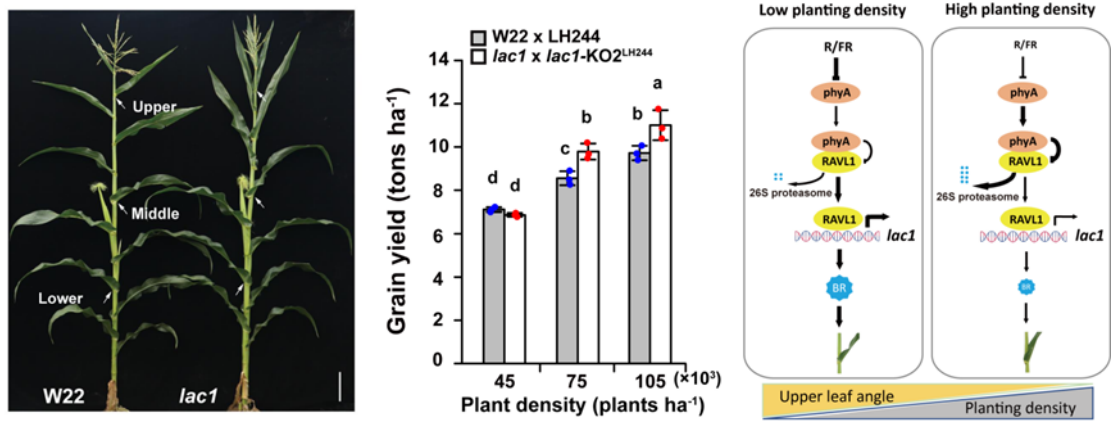


图 1、“智慧株型”基因 *lac1* 促进玉米密植增产。
Figure 1. The *lac1* mutant maize plants display smart-canopy-like plant architecture and increased grain yield at high density.

2、玉米海拔适应性基因位点发掘与演化分析

玉米(*Zea mays* ssp. *mays*)是由约 9000 年前分布在墨西哥西南部巴尔萨斯河流域的大刍草(*Zea mays* ssp. *parviglumis*) 驯化而来。开花期在玉米从热带起源地向温带地区以及由低海拔向高海拔地区传播的过程中发挥了重要作用。先前研究表明, *ZmMADS1* 在玉米开花调控中发挥了重要作用, 但关于该基因如何影响玉米开花期适应性的研究尚未报道。候选基因启动子区关联分析发现, 位于 *ZmMADS1* 上游的 178 bp 的插入缺失与开花期关联性最高($P = 8.91E-05$)(图 1a, c, d), 并且存在单拷贝和双拷贝的单倍型变异, 分别命名为 1xCNV-178 和 2xCNV-178(图 1b)。为了探究 CNV-178 是否在玉米传播过程中发挥作用, 利用来源广泛的 1008 份玉米地方种进行单倍型分析(图 1e)。结果显示, 在纬度分布上, 两个等位基因在南北美洲的分布均没有差异(图 1f,g); 在海拔分布上, 早花单倍型 1xCNV-178 在南北美洲均倾向于分布在高海拔地区, 而晚花单倍型 2xCNV-178 倾向于分布在低海拔地区(图 1h,i)。进一步等位基因频率分析显示, 在南北美洲, 随着海拔的升高, 早花单倍型 1xCNV-178 的等位基因频率表现为上升趋势, 且在海拔高度达 3000 米以上的北美洲地区, 1xCNV-178 的等位基因频率达到了 100%(图 1j)。以上结果表明, 早花单倍型 1xCNV-178 可能在玉米从低海拔地区向高海拔地区传播的过程中发挥了重要的促进作用, 提高了玉米的高海拔地区适应性。

Discovery and Evolutionary Analysis of Maize Altitude Adaptation Gene

Maize (*Zea mays* ssp. *mays*) was domesticated from its wild ancestor, teosinte (*Zea mays* ssp. *parviglumis*), 9,000 years ago in southwestern Mexico. Flowering time has played a significant role in the spread of maize from its tropical origins to temperate regions and from low to high altitudes. *ZmMADS1* was reported to be crucial in the regulation of maize flowering. However, natural variations within this gene and how they mediate maize adaptation across diverse latitudes and



altitudes remain unknown. An association analysis of the 5-kb promoter region revealed a 178-bp insertion-deletion upstream of *ZmMADS1* with the highest association with flowering time ($P = 8.91\text{E-}05$) (Figure 1a, c, d), and the presence of single-copy and double-copy haplotype variations, designated as 1xCNV-178 and 2xCNV-178, respectively (Figure 1b). To investigate the role of CNV-178 in the spread of maize, a haplotype analysis was conducted using 1008 maize landraces. Our findings revealed no difference in the prevalence of two alleles in Americas when considering latitudinal distribution (Figure 1f, g). However, with respect to altitude, we observed a trend where the early-flowering haplotype, 1xCNV-178, was predominantly found in high-altitude regions, whereas the late-flowering haplotype, 2xCNV-178, was more common at lower altitudes (Figure 1h, i). Furthermore, an allele frequency analysis across both Americas showed that the frequency of the early-flowering 1xCNV-178 haplotype increased with altitude. Notably, in North America situated above 3000 meters, the allele frequency of 1xCNV-178 reached 100% (Figure 1j). These findings suggest that the early-flowering haplotype 1xCNV-178 might have played a significant role in facilitating the spread of maize from low to high altitudes, enhancing its adaptability to high-altitude environments.

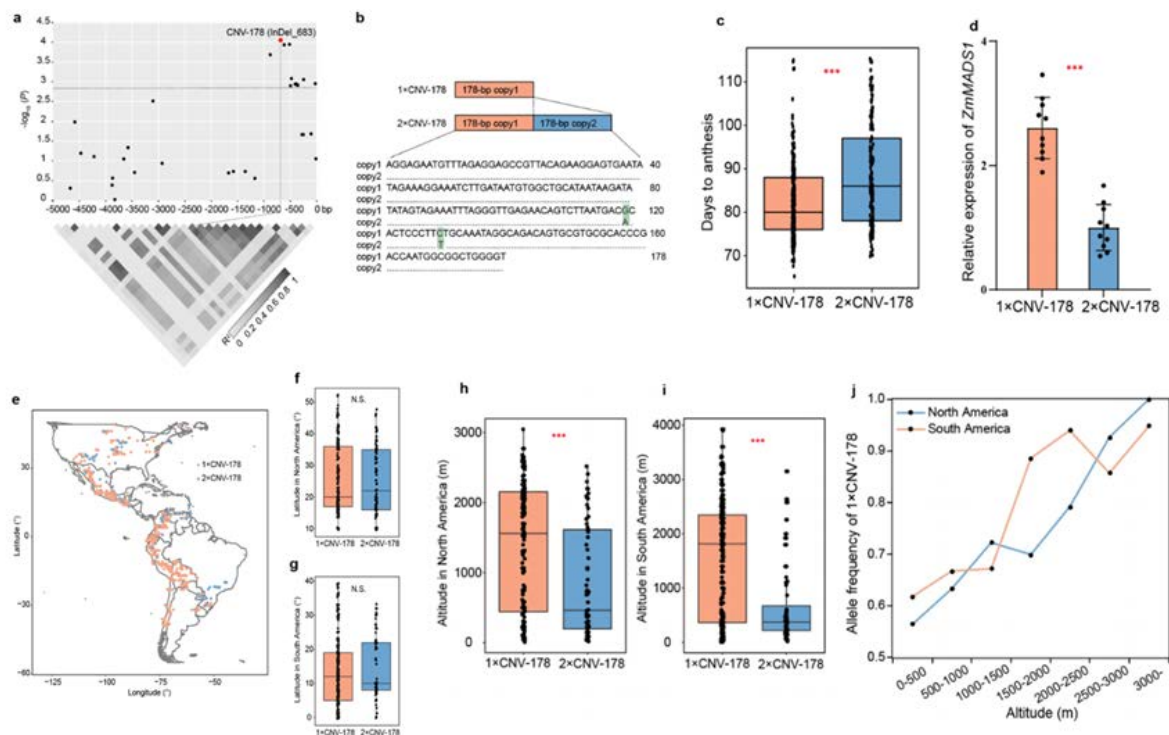


图 2、1xCNV-178 早花单倍型提高玉米高海拔适应性

Figure 2. The early-flowering haplotype 1xCNV-178 enhances adaptability to high-altitude environments in maize.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Tian J[#], Wang C[#], Chen F[#], Qin W, Yang H, Zhao S, Xia J, Du X, Zhu Y, Wu L, Cao Y, Li H, Zhuang J, Chen S, Zhang H, Chen Q, Zhang M, Deng XW, Deng D, Li J^{*}, Tian F^{*} (2024) Maize smart-canopy architecture enhances yield at high densities. **Nature** 632(8025): 576-584.

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研究方向：植物响应胁迫信号的干细胞
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(一) 研究进展

1、综述植物分生组织中干细胞胁迫应答的分子机制

植物分生组织主要包括茎尖端分生组织(Shoot apical meristem, SAM)、根尖分生组织(Root apical meristem, RAM)和形成层分生组织(Vascular cambium)等，植物分生组织的活性对于植物的生长发育具有极其重要的意义。植物胚后生长均来源于分生组织细胞的分裂与分化。环境因素，包括生物和非生物胁迫，以及营养物质的可利用性，影响分生组织的活性，从而影响根和芽乃至整个植株可塑性生长。了解胁迫下分生组织维持的分子机制，将有助于阐明植物适应环境和发育可塑性的调控机制。

周文焜教授和中国科学技术大学赵忠教授团队受邀联合撰写综述，从环境因子、氧化还原调控、生物胁迫和非生物胁迫等四个方面概述了植物分生组织对环境胁迫响应的最新研究进展。本文讨论了植物分生组织适应环境和营养胁迫的信号通路、遗传调节因子和分子机制，以及应激诱导的干细胞功能调节方面取得的进展，包括干细胞微环境中的 DNA 损伤和活性氧调节、伤口愈合和组织修复分子机理，并比较了茎尖和根尖分生组织之间适应环境胁迫的异同及其潜在的分子机制，将有助于阐明植物如何优化营养获取和适应不同的环境条件，深化对植物发育可塑性的了解，并为改善农作物性状和增强耐逆性提供理论依据 (Zeng et al., *Curr Opin Plant Biol*, 2024)。

Tipping the Balance: The Dynamics of Stem Cell Maintenance and Stress Responses in Plant Meristems

Plant meristems contain pools of dividing stem cells that produce new organs for plant growth and development. The activity of plant meristem varies with environmental conditions, such as light/shade and water/nutrient availability. Understanding the molecular mechanism of meristem maintenance under stress will help elucidate the regulatory mechanisms of plant adaptation and developmental plasticity. This article summarizes the latest research progress on the response of plant meristematic tissues to environmental stress from four aspects: environmental factors, redox regulation, biotic and abiotic stress. Understanding how meristem responds to changing environmental conditions will contribute to a better understanding of plant developmental plasticity and provide theoretical basis for improving crop traits and enhancing resistance to stress (Zeng et

al., *Curr Opin Plant Biol*, 2024).

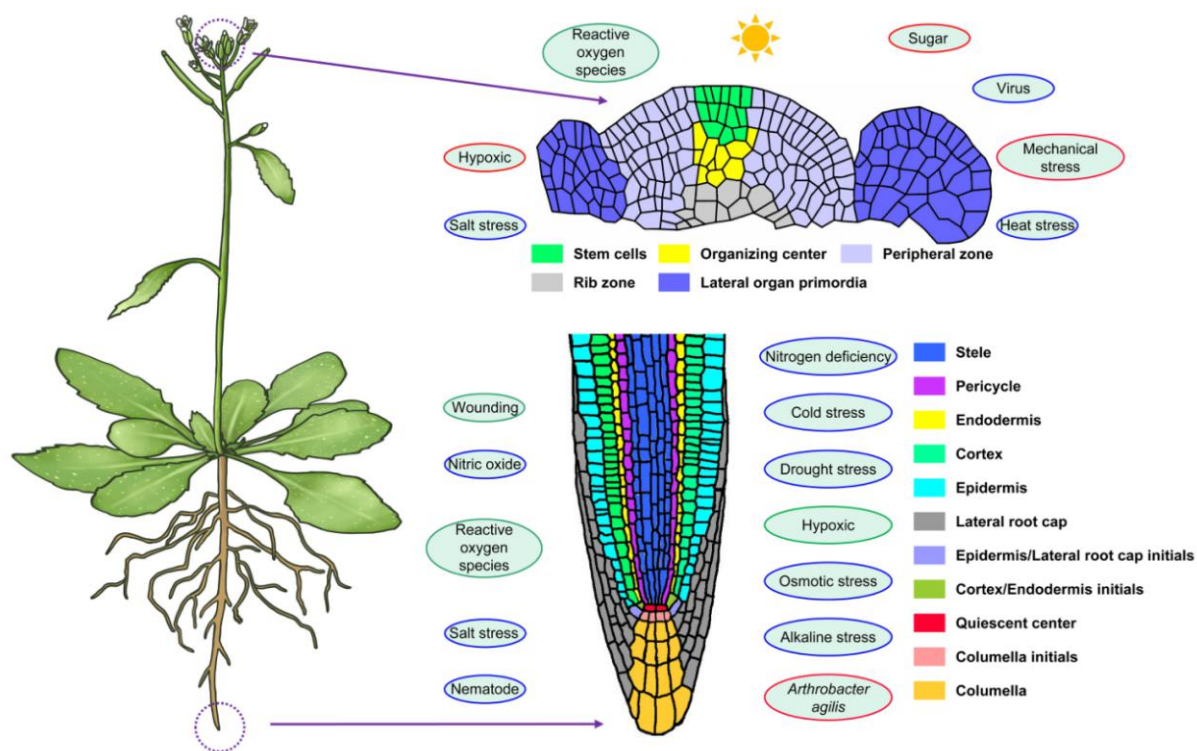


图1、图例植物分生组织及其面临的非生物、生物胁迫。
Figure 1. Illustration of plant meristems, and abiotic and biotic stresses.

2、综述植物再生分子机制研究与应用

与动物再生一样，细胞的全能性和多能性是植物再生的分子基础。植物细胞的全能性和多能性是建立植物高效再生方法的理论基础，相关理论突破将有助于利用基因组编辑技术创造高产、多抗、环境友好的未来作物，从而保证我国和世界农业的绿色可持续发展。

中国农业大学周文焜、中国科学院分子植物科学卓越创新中心王佳伟和华中农业大学陈春丽等13个国内外科研团队受邀联合撰写综述，系统性概述了植物再生分子机制研究与生物技术应用，对植物激素、细胞分裂、表观遗传重塑和转录因子在体细胞重编程和分生组织细胞重建中发挥的作用进行了深入探讨。文章重点介绍了近年来植物再生相关领域的主要研究进展，具体内容包括：1) 植物分生组织概述；2) 根尖分生组织的损伤修复与再生；3) 叶片伤口处根从头再生的细胞和分子基础；4) 拟南芥芽再生；5) 体细胞胚胎发生；6) 原生质体再生；7) 植物再生的进化观；8) 作物再生：从分子机制到应用。最后提出了作物再生应用研究中亟待解决的若干科学问题，总结了促进作物再生的策略和可行性，并提出了提高作物再生效率的未来发展方向 (Chen et al., *Sci China Life Sci*, 2024)。

Plant Regeneration in the New Era: From Molecular Mechanisms to Biotechnology Applications

The totipotency and pluripotency of plant cells are the theoretical basis for establishing efficient regeneration methods in plants. In this paper, we systematically reviewed the recent progress in the analysis of molecular mechanisms of plant regeneration through a variety of controlled regeneration systems and experimental techniques. In addition, the future development direction of improving crop regeneration efficiency was also proposed (Chen et al., *Sci China Life Sci*, 2024).

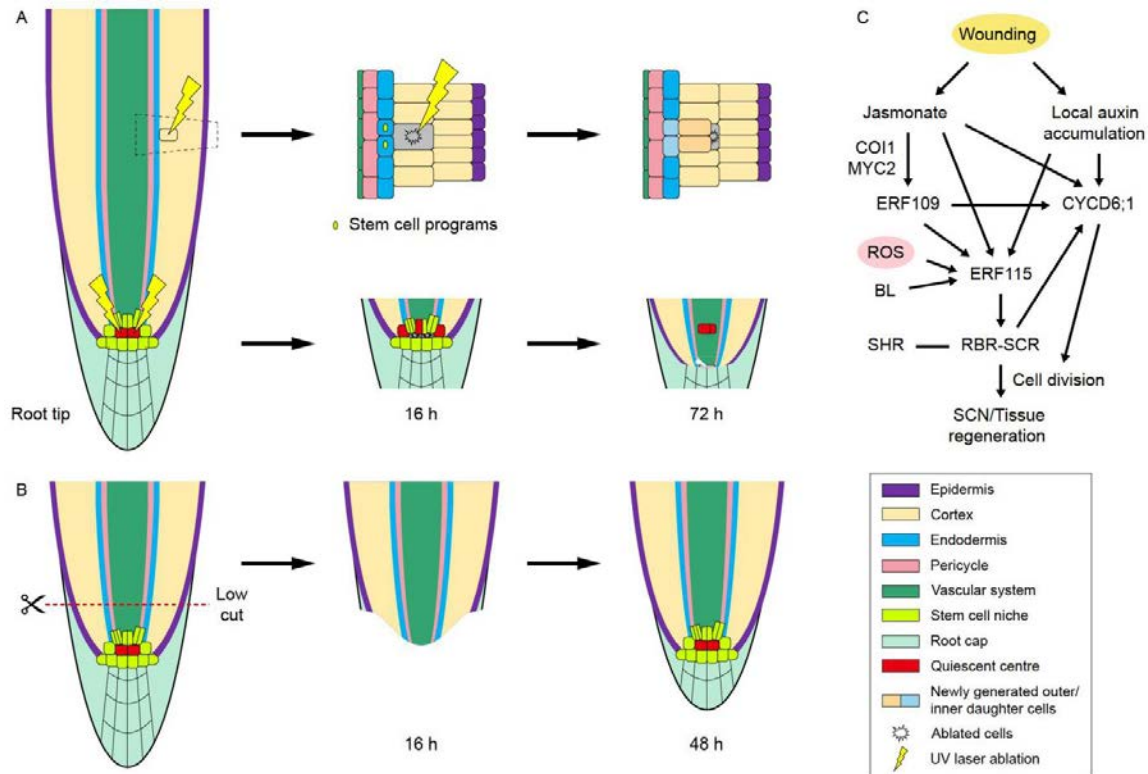


图2、拟南芥根尖分生组织伤口愈合的细胞和分子基础。

Figure 2. Cellular and molecular bases of wound healing in the root apical meristem in *Arabidopsis*.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Zeng J[#], Geng X[#], Zhao Z^{*}, Zhou W^{*} (2024) Tipping the balance: The dynamics of stem cell maintenance and stress responses in plant meristems. *Curr Opin Plant Biol* 78: 102510.
2. Chen C^{*}, Hu Y^{*}, Ikeuchi M^{*}, Jiao Y^{*}, Prasad K^{*}, Su Y^{*}, Xiao J^{*}, Xu L^{*}, Yang W^{*}, Zhao Z^{*}, Zhou W^{*}, Zhou Y^{*}, Gao J, Wang J^{*} (2024) Plant regeneration in the new era: from molecular mechanisms to biotechnology applications. *Sci China Life Sci* 67: 1338-1367.



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王良省，教授。

课题组

研究方向：植物光合作用与活性氧应答。

(一) 研究进展

1、叶绿体单线态氧信号转导模型的修正

叶绿体不但是光合作用的器官，也是一个植物感知环境变化的细胞器，将环境胁迫转变为逆境信号传递到细胞核并调控基因的表达。逆境时，叶绿体中产生过量的活性氧——主要是单线态氧($^1\text{O}_2$)，其通过诱导信号转导级联反应，调控植物胁迫响应。拟南芥 *flu* 突变体能够特异的、可控的产生 $^1\text{O}_2$ 。利用该突变体，发现了叶绿体中 $^1\text{O}_2$ 的 sensor—EX1 蛋白。EX1 位于叶绿体类囊体基粒边缘部位， $^1\text{O}_2$ 介导的 EX1 蛋白降解是诱导 $^1\text{O}_2$ -响应基因表达所必需的。最近有研究报道 $^1\text{O}_2$ 介导 EX1 蛋白从叶绿体转运到细胞核，成熟的 EX1 蛋白在细胞核中与转录因子 WRKY18 和 WRKY40 互作，调控基因表达。我们利用激光共聚焦显微镜发现 $^1\text{O}_2$ 产生后成熟的 EX1 蛋白不在细胞核中积累。而用亚细胞分离技术分离出细胞核时，能够在细胞核组分中检测出 EX1 蛋白。但是，当完整的细胞核组分用蛋白酶 Thermolysin 处理时，EX1 蛋白被降解，细胞核内的组蛋白未被降解。这表明在提取细胞核的过程中，EX1 蛋白粘附在细胞核的外表面，并非是进入到细胞核中，所观察到的 EX1 蛋白在细胞核组分中是细胞器分离过程中造成的假象。在细胞器的分离过程中，叶绿体破裂，很多叶绿体定位的蛋白会泄漏到细胞质中或者黏附在细胞核(或其他细胞器)表面，造成试验假象。同时，我们利用酵母双杂交试验和荧光素酶互补试验也证明全长的 EX1 蛋白并不能与 WRKY18 或者 WRKY40 互作。因此，我们的这项研究证实了 $^1\text{O}_2$ 不能引起 EX1 蛋白进入细胞核中，也不能与细胞核中的 WRKYs 转录因子互作，从而修正了 $^1\text{O}_2$ 信号转导模型，同时证实了分离细胞器验证蛋白定位的方法具有很高假阳性，需要谨慎对待 (Liu et al., *Plant Cell*, 2024)。

Chloroplasts are recognized as environmental sensors, capable of translating environmental fluctuations into diverse signals to communicate with the nucleus. Among the reactive oxygen species produced in chloroplasts, singlet oxygen ($^1\text{O}_2$) has been extensively studied due to its dual roles, encompassing both damage and signaling activities, and the availability of conditional mutants overproducing $^1\text{O}_2$ in chloroplasts. In particular, investigating the *Arabidopsis* (*Arabidopsis thaliana*) mutant known as *fluorescent* (*flu*) has led to the discovery of EXECUTER1 (EX1), a plastid $^1\text{O}_2$ sensor residing in the grana margin of the thylakoid membrane. $^1\text{O}_2$ -triggered EX1 degradation



is critical for the induction of $^1\text{O}_2$ -responsive nuclear genes (SOrNGs). However, a recent study showed that EX1 relocates from chloroplasts to the nucleus upon $^1\text{O}_2$ release, where it interacts with WRKY18 and WRKY40 (WRKY18/40) transcription factors to regulate SOrNG expression. In this study, we challenge this assertion. Our confocal microscopy analysis and subcellular fractionation assays demonstrate that EX1 does not accumulate in the nucleus. While EX1 appears in nuclear fractions, subsequent thermolysin treatment assays indicate that it adheres to the outer nuclear region rather than localizing inside the nucleus. Furthermore, luciferase complementation imaging and yeast 2-hybrid assays reveal that EX1 does not interact with nuclear WRKY18/40. Consequently, our study refines the current model of $^1\text{O}_2$ signaling by ruling out the nuclear relocation of intact EX1 as a means of communication between the chloroplast and nucleus (Liu et al., *Plant Cell*, 2024).

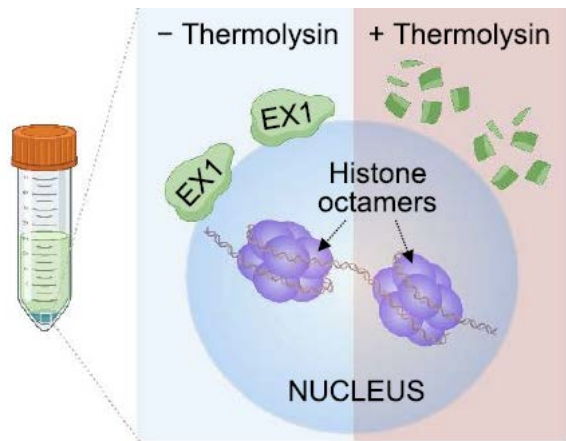


图 1、细胞核提取过程中，部分叶绿体蛋白如 EX1，会粘附在细胞核表面，蛋白酶处理能降解细胞核表面附着蛋白。
Figure 1. Some of the chloroplast proteins adhere to outer envelope of the nucleus during nuclei isolation, and protease treatment degrades these proteins.

2、叶绿体蛋白 TOC33 介导 $^1\text{O}_2$ -EX1 信号转导

叶绿体作为光合作用进行的器官，逆境时其内部会产生过量的活性氧，尤其是单线态氧($^1\text{O}_2$)。拟南芥叶绿体蛋白 EX1 能够通过其 643 位的色氨酸残基(W643)感知叶绿体内 $^1\text{O}_2$ 含量的变化，W643 被氧化后，EX1 蛋白被蛋白酶 FtsH 降解。但是降解的 EX1 蛋白是如何调控细胞核基因表达变化的，还不清楚。拟南芥 *flu* 突变体作为专一性产生 $^1\text{O}_2$ 的工具，我们通过筛选 *flu* 突变体的抑制子，鉴定出 *SOF1* 基因。在 *flu/sof1* 中， $^1\text{O}_2$ 爆发引起的胁迫表型被大幅度抑制。基因克隆表明，*SOF1* 编码叶绿体外膜蛋白 TOC33。*SOF1* 突变后不影响 EX1 蛋白进入叶绿体，不影响其在叶绿体中的定位，不影响 $^1\text{O}_2$ 爆发引起的 EX1 蛋白的降解，但是影响了 $^1\text{O}_2$ 介导的叶绿体到细胞核之间的信号转导。另外，我们发现 1)EX1 蛋白的 UVR 结构域能够和 TOC33 结合，2)在叶绿体外表达 UVR 结构域能够引起 $^1\text{O}_2$ 诱导的 TOC33 依赖的细胞死亡，3)UVR 结构域能够和 WRKYs 转录因子在细胞核中结合，调控基因的表达。本项研究发现了 TOC33 是叶绿体 $^1\text{O}_2$ -EX1 信号途径的下游因子，EX1 蛋白的 UVR 结构域能够替代完整的 EX1 蛋白诱导 $^1\text{O}_2$ 依赖的胁迫响应 (Under revision)。



Chloroplasts engaged in oxygenic photosynthesis frequently overproduce reactive oxygen species (ROS) under stress conditions, with singlet oxygen ($^1\text{O}_2$) being particularly harmful due to its high reactivity and short lifespan. The nuclear-encoded chloroplast protein EXECUTER1 (EX1) detects critical $^1\text{O}_2$ levels through Trp643 oxidation and undergoes proteolysis, a process essential for activating $^1\text{O}_2$ signaling from chloroplasts to the nucleus. However, the link between EX1 proteolysis and subsequent changes in nuclear transcriptome remains unclear. In this study, we isolated *SOF1* (*suppressor of flu 1*) through a forward genetic screen using the *flu* mutant of *Arabidopsis thaliana*, which generates $^1\text{O}_2$ in chloroplasts upon a dark-to-light shift. In the *flu/sof1* mutant, all $^1\text{O}_2$ -induced stress responses are largely suppressed, despite $^1\text{O}_2$ levels being similar to those in the *flu* mutant. *SOF1* encodes the chloroplast outer envelope-anchored preprotein import receptor TOC33. Although TOC33 loss does not affect EX1 import, localization, or $^1\text{O}_2$ -induced proteolysis, it blocks $^1\text{O}_2$ -induced chloroplast-to-nucleus retrograde signaling. Additionally, the UVR domain of EX1 (EX1-UVR) interacts with TOC33 in the chloroplast, and ectopic expression of EX1-UVR outside of the chloroplast induces $^1\text{O}_2$ -dependent cell death. Our findings demonstrate that SOF1/TOC33 mediates $^1\text{O}_2$ -EX1 signaling from the chloroplast to the nucleus and that the EX1-UVR domain can substitute for the full-length EX1 protein in this signaling pathway (Under revision).

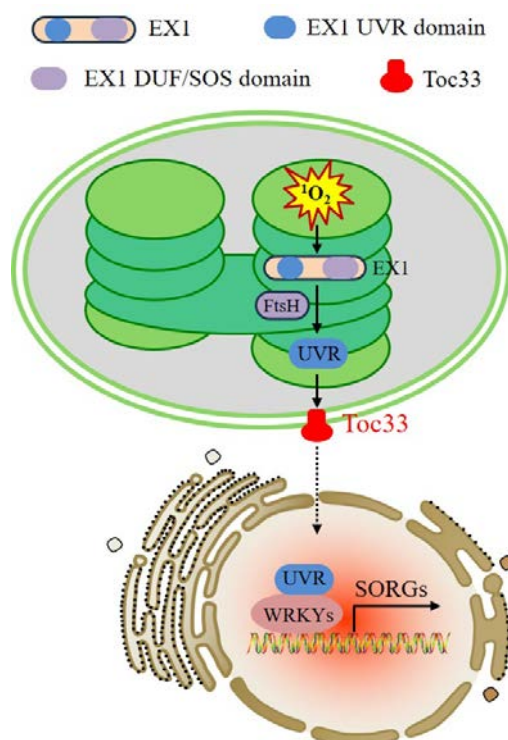


图 2、TOC33 和 EX1-UVR 结构介导叶绿体 $^1\text{O}_2$ 信号转导通路的工作模型。

Figure 2. A proposed model illustrating TOC33 and EX1-UVR in chloroplast $^1\text{O}_2$ -induced signaling.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Liu K, Zhao H, Lee K, Yu Q, Di M, Wang L, Kim C* (2024) EXECUTER1 and singlet oxygen signaling: A reassessment of nuclear activity. *Plant Cell* (1): koae296.

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**徐 凌****课题组**

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研究方向: 作物与微生物组在逆境下的
互动机制。

(一) 研究进展

根系微生物群落抗玉米茎腐病机制研究

微生物组能够增强植物免疫并促进宿主的健康生长, 但其在调控作物抗病机制中的具体作用尚不明确。茎腐病是导致全球玉米减产的主要病害之一, 然而微生物群落在玉米抗茎腐病中的作用尚未得到深入研究。我们的研究发现, 玉米自交系的抗茎腐病能力依赖于微生物群落。病原菌诱导一系列代谢物在玉米抗茎腐病自交系的根部积累, 这些物质不仅能降低病原菌的侵染率, 同时促进了抗病微生物群落在根际的富集。而富集的微生物群落还能够激活植物免疫相关基因的应答, 从而进一步增强宿主的抗病能力。我们的研究表明, 微生物组能够调节并扩展植物的免疫系统, 从而提升植物的抗病能力。基于此, 我们的合成菌群有望在未来的农业生产中应用, 以增强作物的抗病能力。

A Comprehensive Exploration of Maize-Resistant Root-Derived Syncom in Conferring Resistance to Stalk Rot Disease

The microbiome can enhance plant immunity and promote healthy growth of the host, but its specific role in regulating crop disease resistance mechanisms remains unclear. Stalk rot is one of the major diseases causing global maize yield loss, yet the role of microbial communities in maize resistance to stalk rot has not been thoroughly investigated. Our study found that the disease resistance of maize inbred lines to stalk rot depends on the microbiome. Pathogens induce the accumulation of a range of metabolites in the roots of maize inbred lines resistant to stalk rot. These substances not only inhibit pathogen infection but also promote the enrichment of beneficial endospheric microbial communities. The enriched microbial communities can further activate the expression of genes involved in the plant's immune response, thereby enhancing the host's disease resistance. Our research demonstrates that the microbiome can modulate and expand the plant immune system, thereby improving disease resistance. Based on these findings, our synthetic microbial community holds promise for future agricultural applications to improve crop disease resistance.



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研究方向：植物病毒与寄主植物的相互作用的分子机制。

(一) 研究进展

1、MC4-La1 切割模块促进 R-motif 介导的防御基因 mRNA 翻译从而抑制病毒侵染的分子机制研究

植物 metacaspase 家族蛋白是一类结构和功能上与动物 caspase 蛋白酶相似的半胱氨酸蛋白酶，在生物和非生物胁迫中发挥重要的功能。逆境胁迫时，生长相关基因 mRNA 的翻译受抑制，而一些含有 R-motif (5'UTR 具有富含嘌呤的基序) 的防御基因 mRNA 进行不依赖于帽子的翻译，进而抑制病原物的侵染。但是关于 metacaspase 蛋白和 R-motif 介导的防御基因 mRNA 的翻译是否参与植物抗病毒免疫目前尚不清楚。本研究发现大麦条纹花叶病毒 (*barley stripe mosaic virus*, BSMV) 侵染会激活 MC4，进而切割 RNA 结合蛋白 La1。切割后的产物 La1_{ΔC} 亚细胞定位发生改变，从细胞核转位到细胞质。进一步的研究表明切割后的产物 La1_{ΔC} 可以结合到含有 R-motif 的防御基因 mRNA 上，促进 R-motif 介导不依赖帽子的翻译，从而激活植物抗病毒免疫。在本生烟 (*Nicotiana benthamiana*) 超表达 MC4 蛋白显著抑制了 BSMV 的侵染，而敲除 MC4 基因或者敲低 La1 基因的本生烟更易感染不同类型的植物病毒。为反击寄主的防御反应，BSMV 编码的 γ B 蛋白通过与 MC4 互作抑制 MC4 对 La1 的切割。综上所述，该研究揭示了 MC4-La1 切割模块通过促进 R-motif 介导的防御基因 mRNA 的翻译，从而正调控植物抗病毒免疫的全新机制。

The MC4-La1 Cleavage Module Restricts Plant Virus Infection by Integrating R-Motif-Mediated Defense Mrna Translation

The plant cysteine proteases metacaspases are structural homologs of animal caspases and play pivotal roles under biotic and abiotic stresses. However, whether metacaspases and purine-rich elements (R-motif)-mediated defense mRNA translation are involved in plant antiviral immunity remains elusive. Here, we report that barley stripe mosaic virus (BSMV) infection activates metacaspase 4 (MC4) to cleave the RNA binding protein La1. The cleaved La1_{ΔC} version relocates from the nucleus to cytoplasm and promotes the R-motif-mediated cap-independent defense mRNA translation. Moreover, MC4 overexpression significantly restricts BSMV infection in

Nicotiana benthamiana, whereas the knockout of *MC4* and the knockdown of *La1* are more susceptible to diverse plant virus infection. To counteract plant defense, the BSMV *yb* protein directly interacts with *MC4* and inhibits *La1* cleavage. Collectively, our findings unveil a hitherto unknown defense mechanism whereby the *MC4-La1* cleavage module inhibits virus infection by coordinating R-motif-mediated defense mRNA translation.

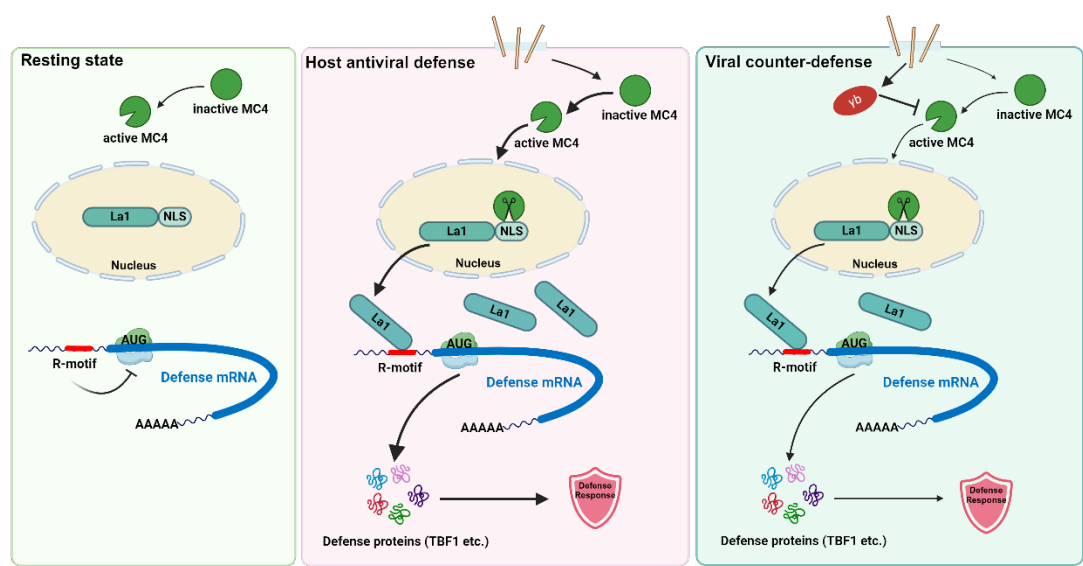


图 1、MC4-La1 模块调控 R-motif 介导的防御基因翻译抑制病毒侵染和 *yb* 蛋白反防御的分子模型。

Figure 1. A proposed model for illustrating MC4-La1 module-mediated antiviral defense and counter defense strategy employed by BSMV.

2、病毒蛋白延缓氧化应激态叶绿体降解以维持病毒侵染的分子机制

叶绿体作为植物光合作用和感知环境变化的细胞器，维持其稳态对植物正常的生长发育和对环境的适应性具有重要的意义。植物病毒，尤其是在叶绿体上复制的病毒，在侵染过程中通常会引起叶绿体的形态变化并影响其生物学功能，但病毒编码蛋白是否可以调控叶绿体的稳态以维持病毒的持续侵染仍未知。我们的研究发现，叶绿体相关蛋白 (chloroplast-related gene 1, *CRG1*) 作为叶绿体稳态的正调控因子，在叶绿体处于氧化应激时，通过增强叶绿体外膜蛋白泛素化进而促进其降解，破坏叶绿体的正常形态和功能，进一步导致叶绿体通过类似微自噬的途径被降解。而当大麦条纹花叶病毒 (BSMV) 侵染时，其编码的 *yb* 蛋白能够直接与 *CRG1* 互作并抑制其活性，从而增加了叶绿体外膜蛋白的稳定性，并抑制了叶绿体细胞器的降解，为病毒提供了一个稳定的复制场所，维持了病毒的持续侵染。

A Viral Protein Delays the Overoxidized Chloroplast Degradation to Finetune Defense-Infection Trade-Offs

Chloroplast is the prototypic organelles that responsible for photosynthesis and environmental sensing. Maintaining the redox homeostasis of chloroplast is vital for plant development and adaptation. However, the structure and function of chloroplasts are usually compromised during plant virus infection. The mechanisms by which viral factors regulate chloroplast homeostasis to maintain infection remain obscure. Here, we identified that the chloroplast-related gene (CRG1) functions as a new positive regulator of chloroplast stability in response to oxidative stress by enhancing the ubiquitination and degradation of chloroplast outer membrane proteins (Toc proteins). Subsequently, the outer membrane-destroyed chloroplasts were degraded by a microautophagy-like pathway that indispensable with the canonical autophagy pathway. During barley stripe mosaic virus (BSMV) infection, the multifunctional protein *yb*, but not its mutant *yb*_{E24A}, directly interacts with CRG1, thus inhibits the degradation of chloroplast and Toc proteins to sustaining viral infection. Our findings reveal a novel role for CRG1 in regulating chloroplast protein stability and homeostasis, as well as the strategy that plant RNA virus protects their replication site to establish an effective infection.

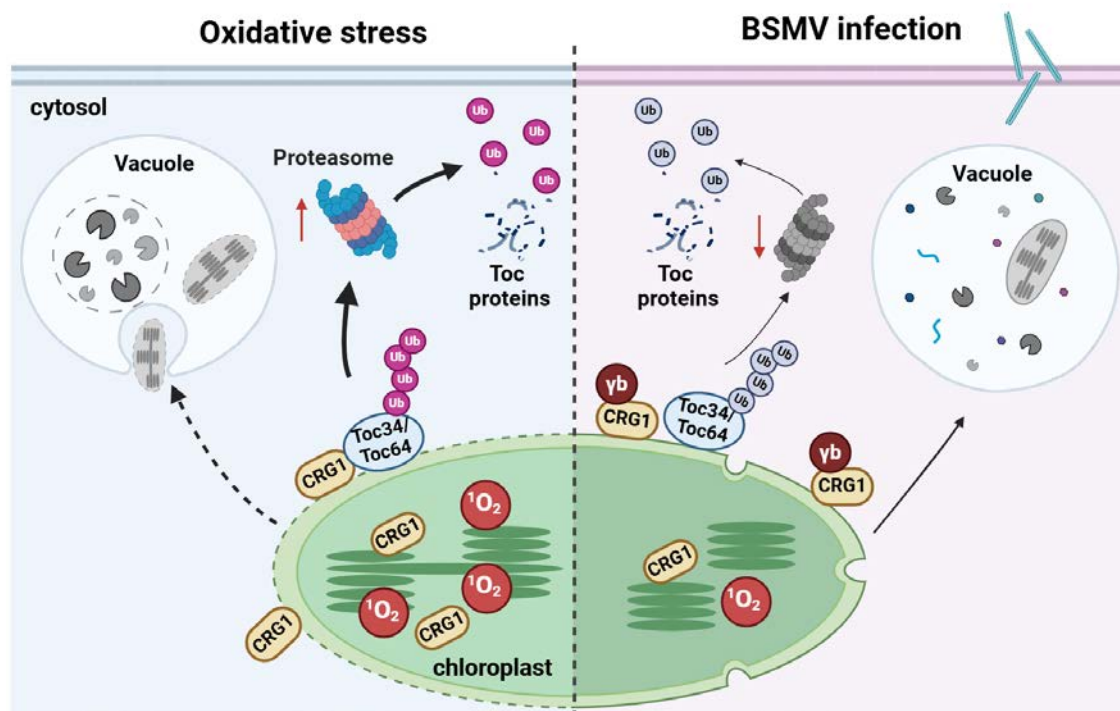


图 2、CRG1 介导叶绿体外膜降解促进叶绿体细胞器降解及病毒蛋白抑制 CRG1 维持叶绿体稳定的工作模型。

Figure 2. A proposed model for illustrating CRG1-mediated degradation of oxidized chloroplast and counter-defense strategy employed by BSMV.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Yue N, Jiang Z, Pi Q, Yang M, Gao Z, Wang X, Zhang H, Wu F, Jin X, Li M, Wang Y, Zhang Y, Li D* (2024) Zn²⁺-dependent association of cysteine-rich protein with virion orchestrates morphogenesis of rod-shaped viruses. *PLoS Pathog* 20(6): e1012311.

(三) 研究队伍

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**张永亮****课题组**

张永亮, 教授。国家优秀青年科学基金获得者(2021)。

研究方向: 植物病毒与宿主互作和抗病毒免疫。

(一) 研究进展

1、SGT1-NSL1 调控 NLR 蛋白介导植物免疫的分子机制

SGT1 在真核生物界高度保守, 是植物正常生长发育所必需的, 同时作为正调控因子也广泛参与多种 NLR(nucleotide-binding leucine-rich repeat)介导的植物免疫中。然而, 长久以来, SGT1 的分子调控网络在很大程度上仍然未知, 并且在植物免疫激活过程中 SGT1 除了作为辅助伴侣蛋白(co-chaperone)发挥作用之外是否还有其他的生物学功能并不清楚。该研究首先建了一套基于完整型 TurboID 和拆分型 Split-TurboID 的邻近标记载体工具箱。利用这一载体工具箱, 对 SGT1 和 SGT1-HSP90 复合体在静息状态(-p50)和免疫激活状态(+p50)的邻近蛋白组进行了系统分析, 证明了 SGT1 的邻近蛋白在免疫激活前后表现为 SGT1 邻近蛋白群体从与植物生长发育相关到与免疫相关的动态转换。我们选择 NSL1 蛋白进行深入研究。遗传学、细胞生物学和生化结果表明, NSL1 以通过抑制 NPR1 的核质穿梭负调控 N 基因介导的对 TMV 的抗性。免疫激活后 NSL1 的蛋白积累量逐渐下降, 进一步研究结果表明, SGT1 可以与 NSL1 互作并促进 NSL1 经 26S 蛋白酶体进行降解, 并且 SIPK 介导 SGT1 的磷酸化可以增强 SGT1 与 NSL1 的互作并促进 NSL1 降解。此外, 敲除 NSL1 同样加速了其它几种 NLR 介导的细胞坏死反应的发生, 并且这几种 NLR 介导的免疫激活都可以 SGT1 依赖的方式促进 NSL1 发生降解。综上所述, 该研究解析了免疫静息状态下, NSL1 通过干扰 NPR1 核质穿梭来负调控 SA 介导的免疫反应; 免疫激活后, SGT1 通过促进免疫负调控因子 NSL1 经 26S 蛋白酶体进行降解来激活免疫, 且 SGT1-NSL1 模块在多个 NLR 介导的免疫中发挥功能。该研究揭示了 SGT1 的分子调控网络, 并揭示了一个新的协调植物先天免疫的信号转导模块 SGT1-NSL1 (Zhang et al., *Mol Plant*, 2024)。论文发表后, *Molecular Plant* 杂志发表了题为 “The cartography of plant immunity: Proximity labeling puts a novel SGT1–NSL1 regulatory module on the map” 的专评。

Proxitome Profiling Reveals a Conserved SGT1-NSL1 Signaling Module that Activates Nlrmediated Immunity

Suppressor of G2 allele of *skp1* (SGT1) is a highly conserved eukaryotic protein that plays a vital role in growth, development, and immunity in both animals and plants. Although some SGT1 interactors have been identified, the molecular regulatory network of SGT1 remains unclear. SGT1

serves as a cochaperone to stabilize protein complexes such as the nucleotide-binding leucine-rich repeat (NLR) class of immune receptors, thereby positively regulating plant immunity. SGT1 has also been found to be associated with the SKP1-Cullin-F-box (SCF) E3 ubiquitin ligase complex. However, whether SGT1 targets immune repressors to coordinate plant immune activation remains elusive. In this study, we constructed a toolbox for TurboID- and split-TurboID-based proximity labeling (PL) assays in *Nicotiana benthamiana* and used the PL toolbox to explore the SGT1 interactome during pre- and post-immune activation. The comprehensive SGT1 interactome network we identified highlights a dynamic shift from proteins associated with plant development to those linked with plant immune responses. We found that SGT1 interacts with Necrotic Spotted Lesion 1 (NSL1), which negatively regulates salicylic acid-mediated defense by interfering with the nucleocytoplasmic trafficking of non-expressor of pathogenesis-related genes 1 (NPR1) during N NLR-mediated response to tobacco mosaic virus. SGT1 promotes the SCF-dependent degradation of NSL1 to facilitate immune activation, while salicylate-induced protein kinase-mediated phosphorylation of SGT1 further potentiates this process. Besides N NLR, NSL1 also functions in several other NLR-mediated immunity. Collectively, our study unveils the regulatory landscape of SGT1 and reveals a novel SGT1-NSL1 signaling module that orchestrates plant innate immunity (Zhang et al., *Mol Plant*, 2024).

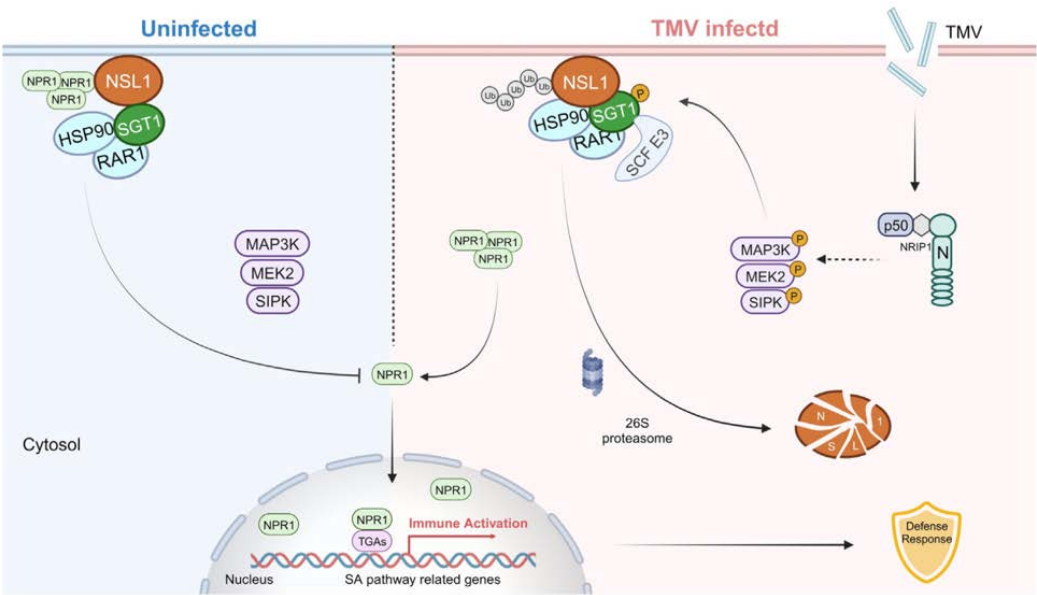


图 1、SGT1-NSL1 调控 NLR 蛋白介导植物免疫的分子模型。

Figure 1. A proposed model for illustrating the functional role of SGT1-NSL1 module in N-mediated resistance against TMV.

2、RH20 通过与 SGS3/RDR6 bodies 互作正调控 RNAi 介导的抗病毒免疫的分子机制

植物为保护自身免受病毒攻击进化出了多种抗病毒防御途径，其中最常见是 RNAi 介导的抗病毒免疫。本研究在 BSMV 病毒基因组 RNAy 编码的 yb 蛋白的 C 端融合了 TurboID 蛋白，利用该载



体鉴定了在病毒侵染条件下 γb 的邻近蛋白组，生物信息分析表明约三分之一的蛋白都和 RNA 加工过程相关，而其中 DEAD-box 家族蛋白重现频率高，进一步选择了 RH20 蛋白进行了深入研究。RNA 沉默抑制子分析和小 RNA 测序证明了 RH20 蛋白促进 RNAi 过程，是 RNA 沉默通路的正调控因子。进一步细胞生物学和生化等实验表明，RH20 通过和 SGS3 直接互作定位到 SGS3/RDR6 小体中，通过增强病毒来源的小干扰 RNA 的产生来负调控 BSMV 的侵染。此外，RH20 还能抑制芜菁花叶病毒(TuMV)、黄瓜花叶病毒(CMV)和甜菜黑色焦枯病毒(BBSV)等病毒的侵染，表明 RH20 在正义链 RNA 病毒侵染中广泛发挥作用。BSMV 的多功能蛋白 γb 很早就被证明具有强烈的 VSR 活性 (Bragg and Jackson, 2004)，然而迄今为止， γb 蛋白发挥 VSR 功能的分子机制仍然未知。为分析 γb 蛋白是否会通过靶向 RH20 蛋白来抑制寄主 RNA 沉默，利用病毒突变体接种实验和竞争性互作实验，证明 γb 蛋白通过干扰 RH20 和 SGS3 的互作来破坏 RH20 的抗病毒功能。该研究鉴定了 RNAi 通路的一个潜在新组分—RH20，该蛋白与 SGS3 互作从而正调控 RNAi 介导的抗病毒免疫；而 BSMV 编码的沉默抑制子 γb 竞争性地破坏 RH20-SGS3 的互作，从而帮助病毒实现反防御 (Wen et al., *Plant Biotechnol J*, 2024)。

DEAD-Box RNA Helicase RH20 Positively Regulates Rnai-Based Antiviral Immunity in Plants by Associating with SGS3/RDR6 Bodies

RNA silencing plays a crucial role in defending against viral infections in diverse eukaryotic hosts. Despite extensive studies on core components of the antiviral RNAi pathway such as DCLs, AGOs and RDRs proteins, host factors involved in antiviral RNAi remain incompletely understood. In this study, we employed the proximity labelling approach to identify the host factors required for antiviral RNAi in *Nicotiana benthamiana*. Using the barley stripe mosaic virus (BSMV)-encoded cb, a viral suppressor of RNA silencing (VSR), as the bait protein, we identified the DEAD-box RNA helicase RH20, a broadly conserved protein in plants and animals with a homologous human protein known as DDX5. We demonstrated the interaction between RH20 and BSMV cb. Knockdown or knockout of *RH20* attenuates the accumulation of viral small interfering RNAs, leading to increased susceptibility to BSMV, while overexpression of *RH20* enhances resistance to BSMV, a process requiring the cytoplasmic localization and RNA-binding activity of RH20. In addition to BSMV, RH20 also negatively regulates the infection of several other positive-sense RNA viruses, suggesting the broad-spectrum antiviral activity of RH20. Mechanistic analysis revealed the colocalization and interaction of RH20 with SGS3/RDR6, and disruption of either SGS3 or RDR6 undermines the antiviral function of RH20, suggesting RH20 as a new component of the SGS3/RDR6 bodies. As a counter-defence, BSMV cb VSR subverts the RH20-mediated antiviral defence by interfering with the RH20–SGS3 interaction. Our results uncover RH20 as a new positive regulator of antiviral RNAi and provide new potential targets for controlling plant viral disease (Wen et al., *Plant Biotechnol J*, 2024).

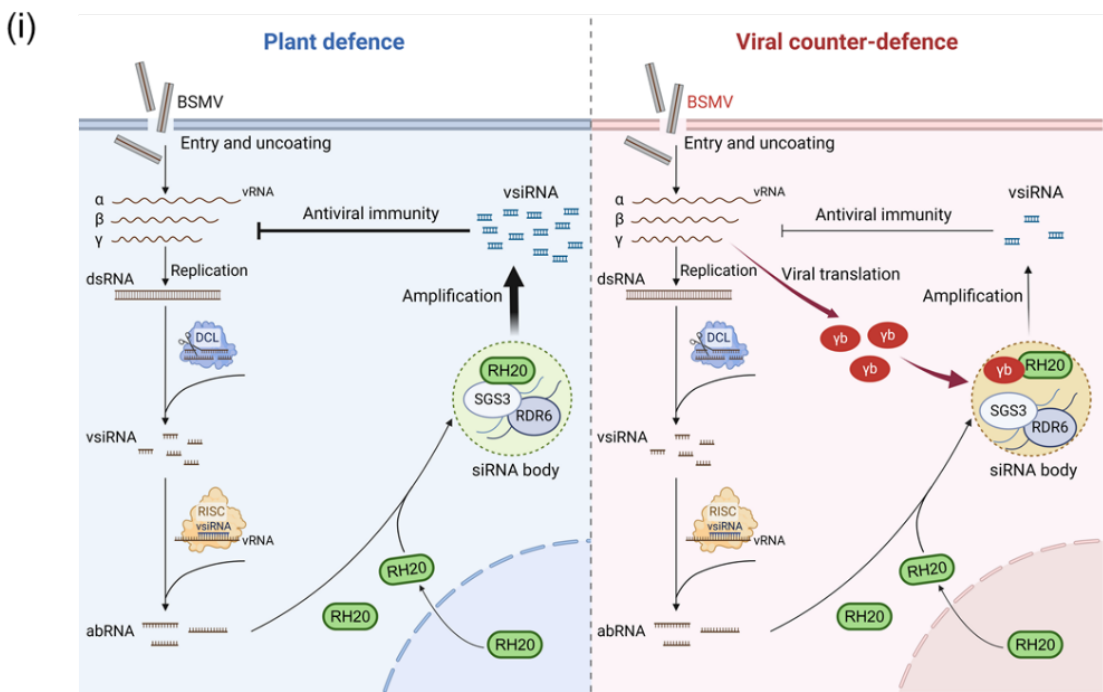


图2、RH20与SGS3/RDR6小体(siRNA body)交互正调控RNAi来抑制BSMV侵染的机制模型。
Figure 2. A proposed model illustrating the mechanism of RH20 to interact with SGS3/RDR6 body (siRNA body) to positively regulate RNAi to inhibit BSMV infection.

3、综述翻译后修饰协同调控呼吸爆发氧化酶 (RBOHs) 产生 ROS

目前已报道多种翻译后修饰(Post-translational modifications, PTMs)参与调控RBOHs的功能，其中包括磷酸化修饰、泛素化修饰、过硫化修饰以及亚硝基化修饰等，这些磷酸化修饰可以调控RBOHs的酶活、蛋白稳定性或亚细胞定位等从而调控ROS的产生，调节植物应对生物胁迫和非生物胁迫的响应。并且PTMs之间存在交互作用，精细调控RBOHs活性的“开”和“关”。该综述系统总结了植物在应对生物胁迫和非生物胁迫时，多种翻译后修饰(Post-translational modifications, PTMs)调控RBOHs功能的分子机制及翻译后之间的交互作用，总结出了“Modification Activation→Brake”模型：RBOHs在健康植株中处于低磷酸化修饰的状态以产生低水平的ROS来维持植物正常生长发育，一旦感知到病原侵染，RBOHs可以发生磷酸化修饰、过硫化修饰以结合磷脂酸(PA)，此外胞内钙离子浓度的增加还可以进一步促进RBOHs磷酸化，从而使得植物能够快速产生ROS以响应外界胁迫；当植物逐渐适应外界胁迫或胁迫减弱后，RBOHs可能会受到泛素化和亚硝基化等修饰的调控，从而抑制其酶活，实现对RBOHs产生ROS的“刹车”。总之，该综述详细总结了RBOHs翻译后修饰调控ROS产生的最新进展，为后续RBOHs相关的研究提供了重要的参考 (Zhang et al., *New Phytol*, 2024)。

Orchestrating ROS Regulation: Coordinated Post-Translational Modification Switches in NADPH Oxidases

Reactive oxygen species (ROS) are among the most important signaling molecules, playing a significant role in plant growth, development, and responses to various environmental stresses. Respiratory burst oxidase homologs (RBOHs) are key enzymes in ROS production. Plants tightly regulate the activation and deactivation of RBOHs through various post-translational modifications (PTMs), including phosphorylation, ubiquitination, S-nitrosylation, and persulfidation. These PTMs fine-tune ROS production, ensuring normal plant growth and development while facilitating rapid responses to abiotic and biotic stresses. This review discusses the effects of different PTMs on RBOH function and their biological relevance. Additionally, we examine the evolutionary conservation of PTM sites and emphasize the complex interplay between multiple PTMs regulating RBOHs (Zhang et al., *New Phytol*, 2024).

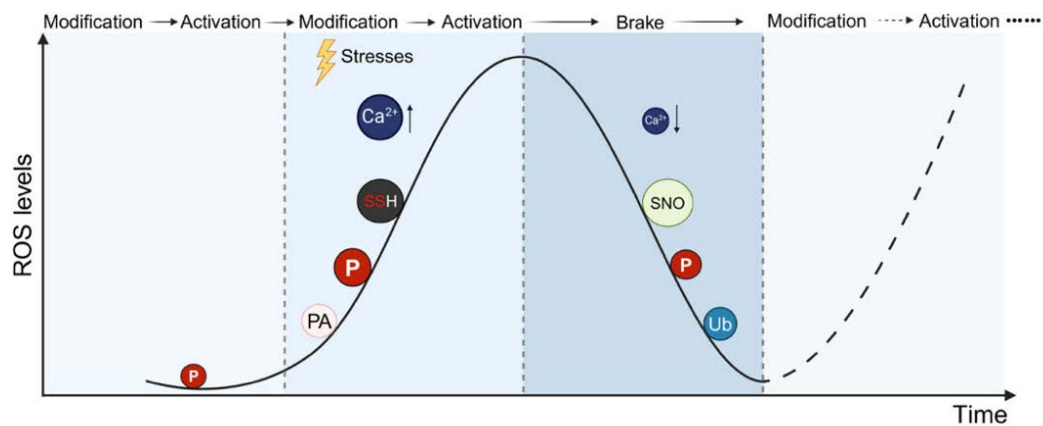


图3、通过翻译后修饰调节RBOH介导ROS产生的“修饰⇌激活→刹车”模型。

Figure 3. A proposed 'Modification ⇌ Activation → Brake' cycle model for regulating RBOH-mediated ROS production through PTMs.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Zhang D#, Yang Y#, Wen Z#, Li Z, Zhang X, Zhong C, She J, Zhang Q, Zhang H, Li W, Zhao X, Xu M, Su Z, Li D, Dinesh-Kumar SP*, Zhang Y* (2024) Proximate profiling reveals a conserved SGT1- NSL1 signaling module that activates NLR-mediated immunity. *Mol Plant* 17: 1369–1391.
2. Wen Z, Hu R, Pi Q, Zhang D, Duan J, Li Z, Li Q, Zhao XY, Yang M, Zhao X, Liu D, Su Z, Li D, Zhang Y* (2024) DEAD-box RNA helicase RH20 positively regulates RNAi-based antiviral immunity in plants by associating with SGS3/RDR6 bodies. *Plant Biotechnol J* DOI: 10.1111/pbi.14448.



3. Zhang X[#], Zhang D[#], Zhong C, Li W, Dinesh-Kumar SP, Zhang Y* (2024) Orchestrating ROS regulation: Coordinated post-translational modification switches in NADPH oxidases. **New Phytol** DOI: 10.1111/nph.20231.
4. Yang Z, Li G, Zhang Y, Li F, Zhou T, Ye J, Wang X, Zhang X, Sun Z, Tao X, Wu M, Wu J, Li Y* (2024) Crop antiviral defense: Past and future perspective. **Sci China Life Sci** DOI: 10.1007/s11427-024-2680-3.
5. Yue N, Jiang Z, Pi Q, Yang M, Gao Z, Wang X, Zhang H, Wu F, Jin X, Li M, Wang Y, Zhang Y, Li D* (2024) Zn²⁺-dependent association of cysteine-rich protein with virion orchestrates morphogenesis of rod-shaped viruses. **PLoS Pathog** 20: e1012311.

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研究方向：虫传植物病毒与植物寄主和昆虫介体的互作机制以及病毒载体开发。

(一) 研究进展

植物弹状病毒编码的孔蛋白P9促进昆虫传毒的分子机理

植物弹状病毒主要由昆虫介体以持久增殖的方式传播，其中病毒由昆虫递送到植物细胞后，如何从病毒包膜中释放复制元件并建立侵染的分子机制尚不明确。我们研究发现了细胞质弹状病毒属的病毒编码一类保守的单次跨膜小蛋白，由 45~70 氨基酸组成，这类蛋白具有病毒孔蛋白序列特征。以植物细胞质弹状病毒大麦黄条纹花叶病毒 (*Barley yellow striate mosaic virus*, BYSMV) 的 P9 孔蛋白为研究对象，发现 P9 能够增加细菌细胞膜通透性，并在酵母互补实验中具有钾离子通道活性。和野生型病毒相比，孔蛋白 P9 的缺失突变体不影响病毒在介体灰飞虱中的侵染增殖，但在健康植物中不能建立侵染。体外实验证明，BYSMV 病毒粒子在 200 mM 钾离子的条件下，才能有效转录病毒 mRNA；同时发现 BYSMV 侵染后能够增加寄主植物 K^+ 水平，进一步促进病毒侵染。本研究揭示了植物弹状病毒编码的孔蛋白(viroporin)形成的通道在病毒包膜上介导胞质中钾离子内流，促进病毒释放复制元件建立侵染的分子机制 (图 1)。同时，本研究建立了植物弹状病毒侵染与植物钾离子营养的联系，发现的病毒孔可作为病毒防控的分子靶标。

The Plant Rhabdovirus Viroporin P9 Facilitates Insect-Mediated Virus Transmission in Barley

Potassium (K^+) plays crucial roles in both plant development and immunity. However, the function of K^+ in plant-virus interactions remains largely unknown. Here, we utilized *Barley yellow striate mosaic virus* (BYSMV), an insect-transmitted plant cytorhabdovirus, to investigate the interplay between viral infection and plant K^+ homeostasis. The BYSMV accessory P9 protein exhibits viroporin activity by enhancing membrane permeability in *Escherichia coli*. Additionally, P9 increases K^+ uptake in yeast (*Saccharomyces cerevisiae*) cells, which is disrupted by a point mutation of glycine 14 to threonine (P9G14T). Furthermore, BYSMV P9 forms oligomers and targets to both the viral envelope and the plant membrane. Based on the recombinant BYSMV-GFP (BYGFP) virus, a P9-deleted mutant (BYGFP Δ P9) was rescued and demonstrated infectivity



within individual plant cells of *Nicotiana benthamiana* and insect vectors. However, BYGFPΔP9 failed to infect barley plants after transmission by insect vectors. Furthermore, infection of barley plants was severely impaired for BYGFP-P9G14T lacking P9 K⁺ channel activity. *In vitro* assays demonstrate that K⁺ facilitates virion disassembly and the release of genome RNA for viral mRNA transcription. Altogether, our results show that the K⁺ channel activity of viroporins is conserved in plant cytorhabdoviruses and plays crucial roles in insect-mediated virus transmission.

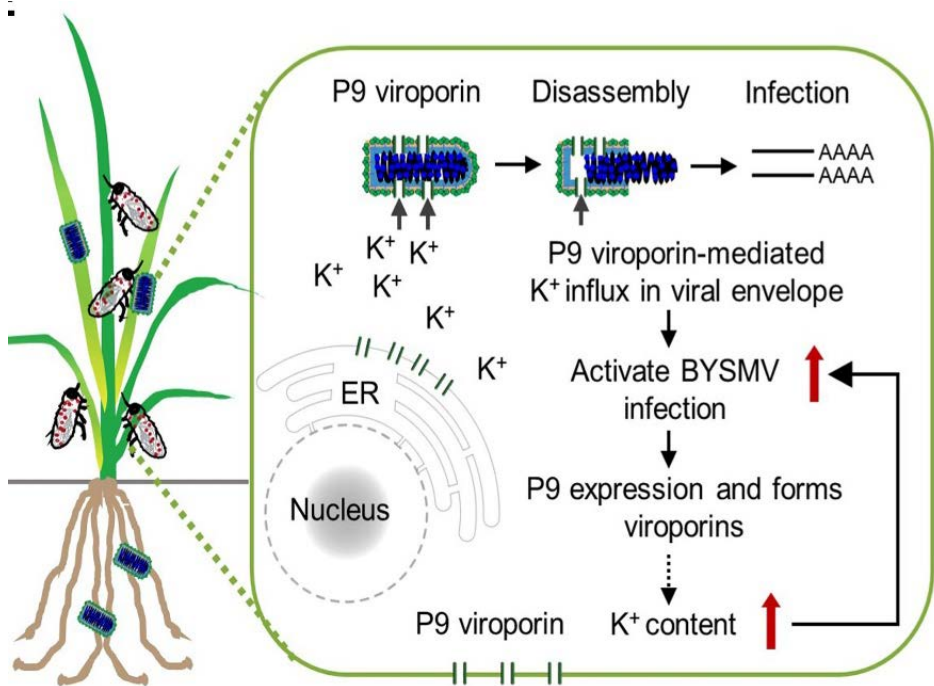


图1、病毒孔P9蛋白调控虫传病毒释放的分子机制。

Figure 1. A potential model of BYSMV P9 viroporin in insect-borne virus infection.

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

Gao Q, Zang Y, Qiao J, Zhang Z, Wang Y, Han C, and Wang X * (2024) The plant rhabdovirus viroporin P9 facilitates insect-mediated virus transmission in barley. *Plant Cell* 36(9): 3483-3497.

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研究方向：根瘤菌共生固氮机制与合成生物学改造。

(一) 研究进展

共适合度网络连接度决定根瘤菌泛基因组的朦胧边界

大多数计算机模拟进化研究通常假定核心基因对细胞功能至关重要，而附属基因则是可有可无的，尤其是在营养丰富的环境中。然而，这一假定很少在泛基因组背景下通过遗传学方法进行验证。在本研究中，我们针对具有典型开放性泛基因组的中华根瘤菌菌株，在营养丰富的培养基中对适合度基因进行了可靠的泛基因组转座子测序(Tn-seq)分析。为评估适合度类别划分的可靠性，我们采用三种方法对每个菌株的三个独立突变体文库的转座子测序数据进行了分析，结果表明基于隐马尔可夫模型(HMM)的方法对突变体文库之间的差异耐受性最强，且对数据量不敏感，优于基于贝叶斯和蒙特卡罗模拟的方法。因此，我们采用隐马尔可夫模型方法对适合度类别进行分类。被归类为生长必需(ES)、生长有利(GA)和生长不利(GD)基因的适合度基因在核心基因中富集，而非必需基因(NE)在附属基因中所占比例高。附属的必需/有利基因相较于核心的必需/有利基因表现出更低的适合度效应。共适合度网络中的连接度按必需(ES)、生长不利(GD)和生长有利/非必需(GA/NE)的顺序依次降低。除附属基因外，3284个核心基因中有1599个在测试菌株中表现出不同的必需性。在泛基因组的核基因组内，共享的准必需(ES和GA)基因以及菌株依赖性适合度基因都富集于相似的功能类别中。我们的分析表明，中华根瘤菌泛基因组中存在一个由共适合度连接度所决定的模糊必需区，共适合度网络对我们理解原核生物泛基因组数据的遗传基础方面具有重要作用 (Zhang et al., *mLife*, 2024)。

Cofitness Network Connectivity Determines a Fuzzy Essential Zone in Open Bacterial Pangenome

Most in silico evolutionary studies commonly assumed that core genes are essential for cellular function, while accessory genes are dispensable, particularly in nutrient-rich environments. However, this assumption is seldom tested genetically within the pangenome context. In this study, we conducted a robust pangenomic Tn-seq analysis of fitness genes in a nutrient-rich medium for *Sinorhizobium* strains with a canonical open pangenome. To evaluate the robustness of fitness category assignment, Tn-seq data for three independent mutant libraries per strain were analyzed by three methods, which indicates that the Hidden Markov Model (HMM)-based method is most robust to variations between mutant libraries and not sensitive to data size, outperforming the



Bayesian and Monte Carlo simulation-based methods. Consequently, the HMM method was used to classify the fitness category. Fitness genes, categorized as essential (ES), advantage (GA), and disadvantage (GD) genes for growth, are enriched in core genes, while nonessential genes (NE) are over-represented in accessory genes. Accessory ES/GA genes showed a lower fitness effect than core ES/GA genes. Connectivity degrees in the cofitness network decrease in the order of ES, GD, and GA/NE. In addition to accessory genes, 1599 out of 3284 core genes display differential essentiality across test strains. Within the pangenome core, both shared quasi-essential (ES and GA) and strain-dependent fitness genes are enriched in similar functional categories. Our analysis demonstrates a considerable fuzzy essential zone determined by cofitness connectivity degrees in *Sinorhizobium* pangenome and highlights the power of the cofitness network in understanding the genetic basis of ever-increasing prokaryotic pangenome data (Zhang et al., *mLife*, 2024).

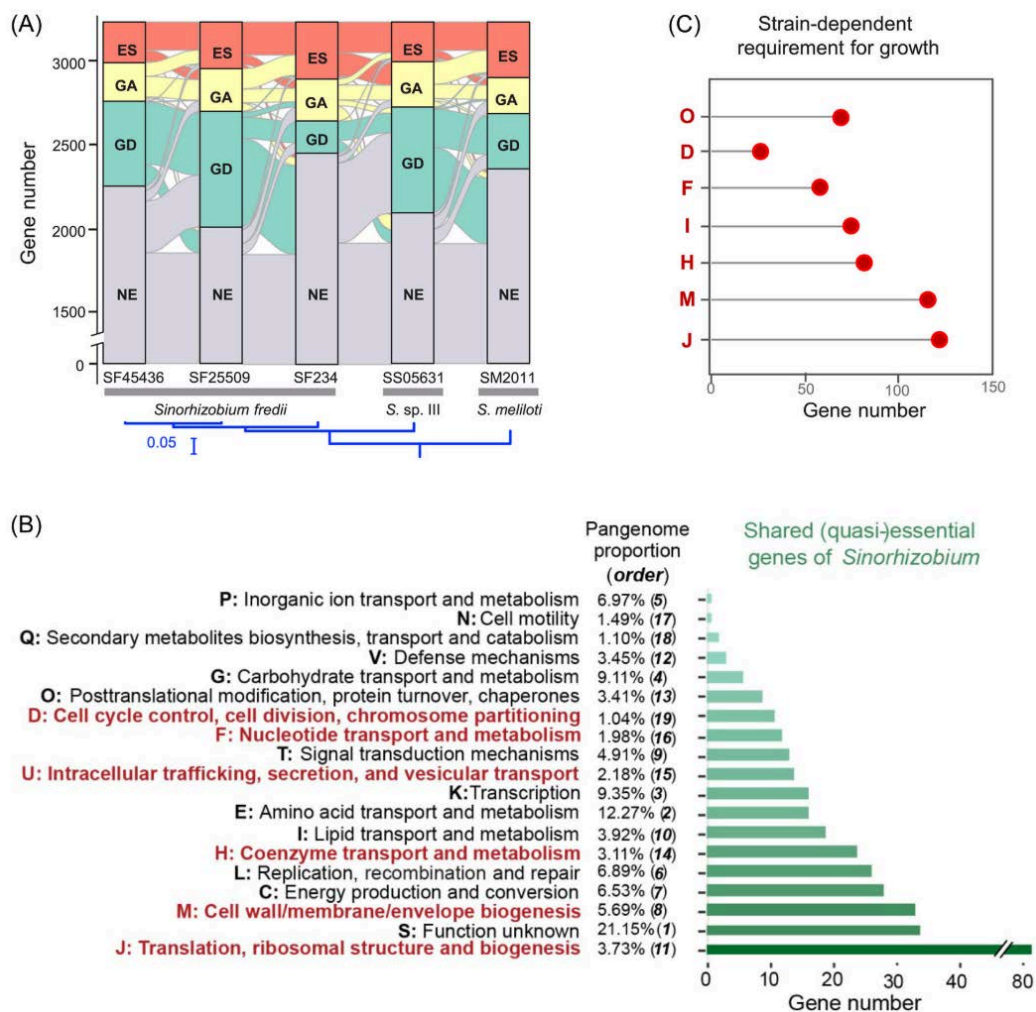


图1、中华根瘤菌属泛基因组必需基因的朦胧边界。

Figure 1. A considerable fuzzy essential zone of *Sinorhizobium* pangenome core.



(二) 研究成果

发表论文: (*Corresponding author)

Zhang P, Zhang B, Ji Y, Jiao J, Zhang Z*, Tian C* (2024) Cofitness network connectivity determines a fuzzy essential zone in open bacterial pangenome. *mLife* 3: 277–290.

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研究方向：通过研究重要农作物性状相关蛋白质结构与功能，为改良农业作物品种提供线索。

(一) 研究进展

1、水稻阳离子转运体 HKTs 在盐胁迫下的结构研究

高亲和钾转运体(HKTs)可选择性地渗透 Na^+ 或 Na^+/K^+ ，在维持植物 Na^+/K^+ 稳态中起关键作用。虽然它们参与耐盐性被广泛报道,但水稻 HKTs 的分子基础仍然难以捉摸。这项研究阐明了 OsHKT1;1 和 OsHKT2;1 的结构，代表了两个不同类别的水稻 HKTs。二聚体组装的 OsHKTs 在结构上可分为四个结构域。在二聚体界面上，第三结构域的半螺旋或环由相反亚基的 c 端区协调。此外，该研究提出了 OsHKT1;5 耐盐和盐敏感变异的 结构，这是一个与耐盐性相关的关键数量性状位点。耐盐变异 OsHKT1;5 表现出增强的 Na^+ 运输能力和更灵活的构象。这些发现揭示了水稻 HKTs 的分子基础，并为它们在耐盐性中的作用提供了见解 (Gao et al., *J Integr Plant Biol*, 2024)。

Structural Insights into the *Oryza Sativa* Cation Transporters Hkts in Salt Tolerance

The high-affinity potassium transporters (HKTs), selectively permeable to either Na^+ alone or Na^+/K^+ , play pivotal roles in maintaining plant Na^+/K^+ homeostasis. Although their involvement in salt tolerance is widely reported, the molecular underpinnings of *Oryza sativa* HKTs remain elusive. In this study, we elucidate the structures of OsHKT1;1 and OsHKT2;1, representing two distinct classes of rice HKTs. The dimeric assembled OsHKTs can be structurally divided into four domains. At the dimer interface, a half-helix or a loop in the third domain is coordinated by the C-terminal region of the opposite subunit. Additionally, we present the structures of OsHKT1;5 salt-tolerant and salt-sensitive variants, a key quantitative trait locus associated with salt tolerance. The salt-tolerant variant of OsHKT1;5 exhibits enhanced Na^+ transport capability and displays a more flexible conformation. These findings shed light on the molecular basis of rice HKTs and provide insights into their role in salt tolerance (Gao et al., *J Integr Plant Biol*, 2024).



2、拟南芥外向整流 K⁺通道转换为内向整流通道的结构变化

本研究利用低温电子显微镜和电生理学，描述了拟南芥中 K⁺外向整流通道 SKOR 的结构和功能动态，以及与将 SKOR 转变为内向整流 K⁺通道 SKDM 的双重突变相关的结构变化。这些发现对于理解和操纵作物 K⁺营养具有重要意义。钾是植物生长所必需的矿物质营养素。植物主要通过根部从土壤或生长介质中吸收 K⁺，并将其重新分配到各个组织中。为了有效地调节 K⁺的吸收和分布，植物拥有复杂的 K⁺转运蛋白和通道网络，以促进 K⁺跨细胞膜的选择性移动。该研究对植物中一种基本的 K⁺输出通道 SKOR 进行了深入的结构和功能分析，并揭示了与其从 K⁺输出通道转变为 K⁺输入通道相关的分子变化。D312N 和 L271P 突变之间的相互作用导致从外向整流转变为内向整流。这种机制可能为控制 K⁺从根部到茎部的分布提供线索。由于 SKOR 同源物的序列在作物中是保守的，这项研究预计可能为开发对 K⁺缺乏具有更高抗性的作物提供指导 (Gao et al., *Plant Commun*, 2024)。

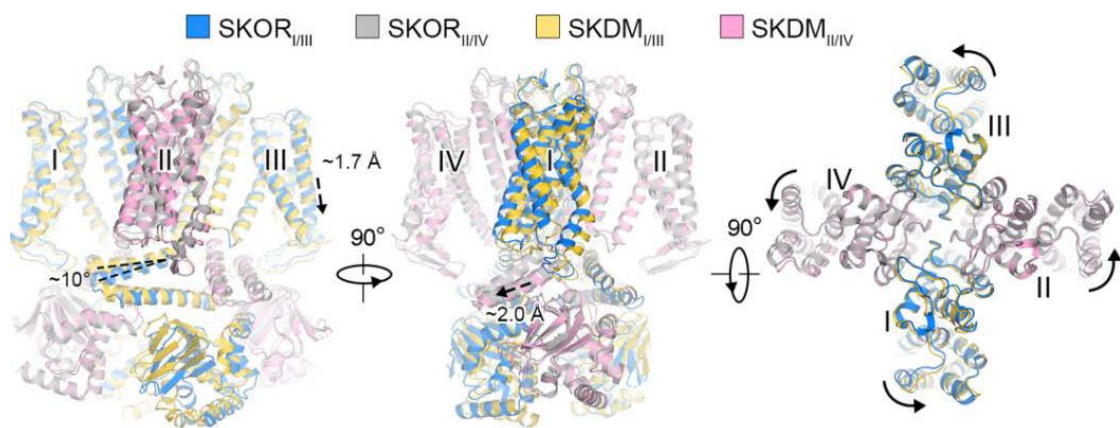


图1、SKOR 和 SKDM 的结构比对。

Figure 1. Structural alignment of SKOR and SKDM.

Structural Changes in the Conversion of an *Arabidopsis* Outward-Rectifying K⁺ Channel into an Inward-Rectifying Channel

By using cryo-electron microscopy and electrophysiology, this study characterizes the structural and functional dynamics of the K⁺ outward-rectifying channel SKOR in *Arabidopsis* and the structural changes associated with a double mutation that transforms SKOR into an inward-rectifying K⁺ channel, SKDM. These findings have implications for understanding and manipulating crop K⁺ nutrition. Potassium is an essential mineral nutrient for plant growth. Plants absorb K⁺ primarily from the soil or growth medium through the roots and redistribute it across various tissues. To efficiently regulate K⁺ uptake and distribution, plants possess a sophisticated network of K⁺ transporters and channels that facilitate the selective movement of K⁺ across cellular membranes. We performed an in-depth structural and functional analysis of SKOR, a fundamental K⁺_{out} channel in plants, and revealed the molecular changes associated with its conversion from a K⁺_{out} channel to a K⁺_{in} channel. The interplay between the D312N and L271P mutations results in a change from



outward to inward rectification. This mechanism may provide clues for controlling the distribution of K^+ from roots to shoots. As the sequences of SKOR homologs are conserved in crops, we anticipate that this study may provide guidance for development of crops with greater resistance to K^+ deficiency (Gao et al., *Plant Commun*, 2024).

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Gao R, Jia Y, Xu X, Fu P, Zhou J, & Yang G* (2024) Structural insights into the *Oryza sativa* cation transporters HKTs in salt tolerance. ***J Integr Plant Biol*** 66(4): 700–708.
2. Gao X, Xu X, Sun T, Lu Y, Jia Y, Zhou J, Fu P, Zhang Y, & Yang G* (2024) Structural changes in the conversion of an *Arabidopsis* outward-rectifying K^+ channel into an inward-rectifying channel. ***Plant Commun*** 5(6):100844.

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研究方向：玉米发育相关基因的功能和作用机制，谷子抗逆基因功能和分子机制。

(一) 研究进展

1、谷子 *SiNAC015* 参与谷子抗旱的功能研究

随着全球变暖和人口增加，缺水引起的干旱胁迫已成为限制农作物生长和产量的关键因素。谷子由于长期种植在干旱和半干旱地区，是研究非生物抗逆性的理想模式作物。该研究发现了谷子中一个受干旱诱导显著上调表达的 NAC 家族转录因子 *SiNAC015*，且该基因被预测为谷子 miR164 的潜在靶基因。苗期土壤干旱处理发现 *sinac015* 敲除突变体具有干旱敏感的表型，复水后存活率显著低于野生型，*SiNAC015* 过表达谷子复水后存活率较野生型高，抗旱性增强。通过 RNA-seq 发现 *SiNAC015* 过表达谷子中能够富集到大量与 ROS 相关的通路，其中包含的基因基本都编码 ROS 清除关键酶过氧化物酶 (POD)，RT-qPCR 分析这些基因在 *SiNAC015* 过表达谷子中显著上调表达，在 *sinac015* 突变体中下调表达。进一步检测 *SiNAC015* 转基因谷子 ROS 积累情况，发现干旱处理后 *SiNAC015* 过表达谷子叶片 DAB 染色较野生型浅， H_2O_2 和 MDA 含量低，POD 酶活增加，*sinac015* 突变体 DAB 染色较深， H_2O_2 和 MDA 显著高于野生型，POD 酶活降低。在 20% PEG 模拟干旱处理生长 7 天的 *SiNAC015* 转基因谷子初生根中也观察到相似表型，表明 *SiNAC015* 通过提高谷子 ROS 清除能力正调控谷子抗旱。该研究揭示了 *SiNAC015* 参与谷子干旱胁迫响应的功能机制，为抗旱育种提供优质基因资源。

Sinac015 Regulates Drought Tolerance via Enhancing ROS Scavenging in Foxtail Millet

With global warming and increasing population, drought stress has become a key factor limiting crop growth and yield. Foxtail millet (*Setaria italica*) is an ideal model crop for studying abiotic resistance due to its long-term cultivation in arid and semi-arid areas. In this study, we identified that *SiNAC015* was significantly upregulated under 20% PEG treatment in foxtail millet and was predicted to be a potential target gene of miR164. The *sinac015* mutant was sensitive to drought stress and showed markedly lower survival rates after rewatering than the wild type (WT), in contrast to *mSiNAC015*-overexpression lines, which exhibited enhanced drought tolerance. A large number of ROS-related terms were enriched in *mSiNAC015*-overexpression lines by RNA-



seq analysis, and most of these genes were predicted to encode peroxidases (POD) involved in ROS scavenging. RT-qPCR revealed that these genes were indeed upregulated in *mSiNAC015*-overexpression lines, but downregulated in *sinac015* mutants compared to the WT. We further detected that the *sinac015* mutant exhibited increased ROS accumulation and decreased POD activity after drought treatment compared to WT, while *mSiNAC015*-overexpression lines showed lower ROS content and higher POD activity, suggesting that SiNAC015 positively regulates drought tolerance by enhancing ROS scavenging.

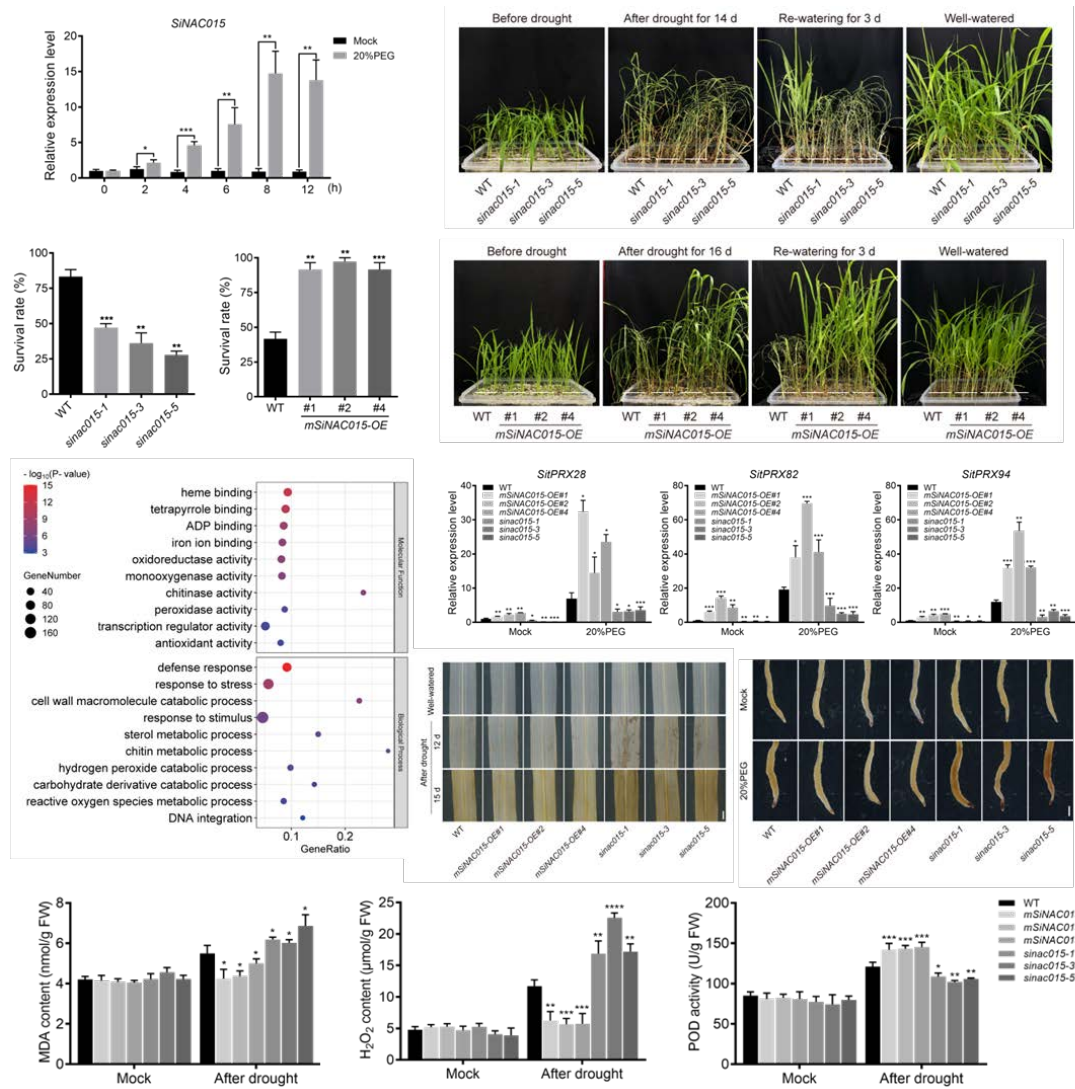


图 1、SiNAC015 参与谷子抗旱的功能研究。
Figure 1. Functional analysis of SiNAC015 in the regulation of drought tolerance in foxtail millet.

2、谷子 SiHsfB2b 响应干旱胁迫的功能研究

植物热激因子 (Heat shock factor, Hsf) 在植物体内广泛存在, 是植物热激响应的关键调节因子。迄今为止, 植物 Hsf 相关的研究报道主要集中于 A 类 Hsf 成员的功能探究, 而 B 类和 C 类的研究较

少。本研究从谷子干旱处理后转录组数据中筛选到一个受干旱诱导上调表达，且自身表达具有节律性的属于 B 类 Hsf 转录因子基因 *SiHsfB2b*。亚细胞定位显示 *SiHsfB2b* 定位于细胞核，且具有转录抑制活性。为了明确 *SiHsfB2b* 在干旱胁迫响应中的功能，对 *SiHsfB2b* 转基因谷子进行苗期土壤干旱处理。在干旱处理 14 天时，*sihsfb2b* 突变体的叶片出现明显萎蔫，脯氨酸含量低于野生型，复水后存活率低于野生型；干旱处理 16 天后，过表达 *SiHsfB2b* 谷子长势仍优于野生型，脯氨酸含量高于野生型，复水后存活率较野生型高，表明 *SiHsfB2b* 正调控谷子苗期抗旱性。

Sihsfb2b, A Class B Heat Shock Factor, Is Involved in Drought Response

Heat shock factors (Hsfs) are key regulators involved in biotic and abiotic stress responses, especially playing a central role in modulating heat tolerance. Based on their structure and function, the plant Hsf family has been divided into three groups, HsfA, HsfB, and HsfC, and the function of HsfA has been extensively studied. In this study, we identified a drought-induced upregulated gene, *SiHsfB2b*, a class B Hsf transcription factor member with rhythmic expression. Subcellular localization revealed that *SiHsfB2b* localized to the nucleus and displayed transcriptional repressive activity. To clarify the function of *SiHsfB2b* in drought response, *SiHsfB2b* transgenic plants grown in soil were subjected to drought treatment at the seedling stage. The *sihsfb2b* mutants were sensitive to drought stress and exhibited significantly lower survival rates after rewatering than the wild type (WT), whereas the *SiHsfB2b*-overexpression lines showed greater drought tolerance, suggesting that *SiHsfB2b* positively regulates drought tolerance in foxtail millet.

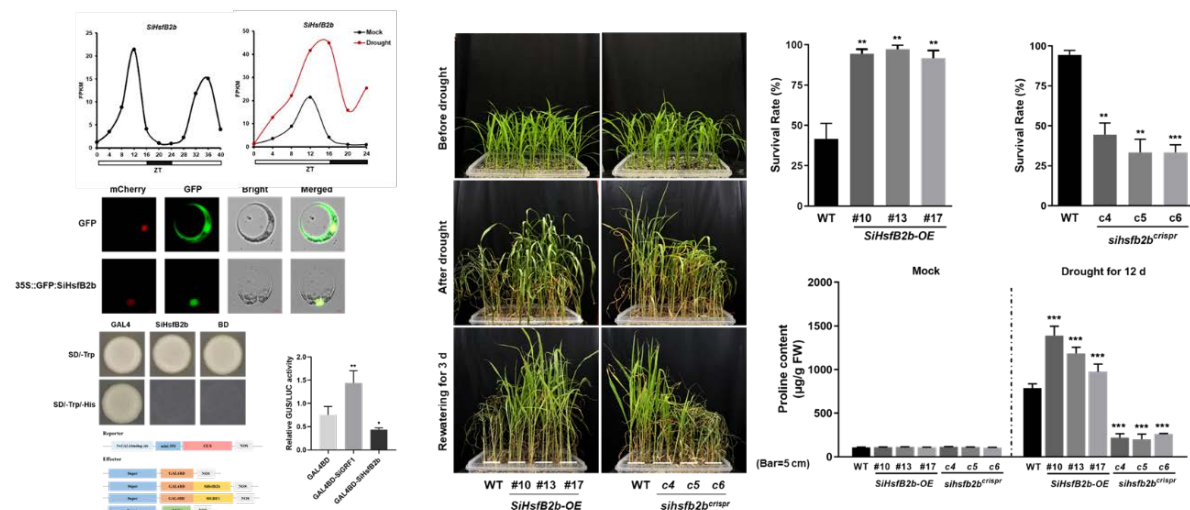


图 2、SiHsfB2b 响应干旱胁迫的功能研究。

Figure 2. Functional analysis of *SiHsfB2b* in drought tolerance of foxtail millet.



(二) 研究成果

专利申请与授权:

谷子 SiHsfB2b 基因在调控谷子抗旱性中的应用; 专利申请号: CN202410974899.0; 申请日期: 2024 年 7 月 19 日。

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研究方向：植物抗病的分子机制。

(一) 研究进展

1、南方锈菌的致病机制

玉米南方锈病是由多堆柄锈菌(*Puccinia polysora* Underw) 引起的全球性真菌病害。近年来，南方锈病在我国各地频繁爆发，造成的经济损失每年高达数十亿元，严重威胁我国玉米生产和粮食安全。鉴于该病害的严重性，自2023年起，农业部已将玉米南方锈病列为一类农作物病害。目前，关于多堆柄锈菌的致病机制研究尚不充分，极大地制约了南方锈病的防治工作。效应蛋白是病原微生物成功侵染宿主作物的关键因子，也是研究病原致病机理的重要切入点。本课题组与合作伙伴通过组装玉米多堆柄锈菌的基因组，并结合侵染过程中的转录组数据，预测出107个候选效应蛋白。利用烟草瞬时表达系统，我们发现其中8个效应蛋白能够显著抑制植物的免疫反应。进一步研究发现，2个效应蛋白在玉米中过表达后，能够明显促进南方锈病的发生，并通过蛋白组学鉴定了与其互作的宿主蛋白。基于此，我们将进一步利用分子生物学、生化以及细胞生物学技术，解析效应蛋白调控宿主靶标的分子机制。

Pathogenic Mechanism of Southern Rust Fungus

Southern corn rust, caused by the fungus *Puccinia polysora* Underw, is a global fungal disease. In recent years, there have been continuous outbreaks of southern rust in various regions of China, leading to annual economic losses of billions of yuan and posing a threat to maize production and food security. Because of the severity of this disease, the Ministry of Agriculture officially classified southern rust as first-level disease from 2023. However, our understanding of the pathogenic mechanisms of *P. polysora* is limited, severely hindering the prevention and control against maize southern rust. Effector proteins play a crucial role in enabling pathogens to successfully infect crops, and are important targets for studying pathogenic mechanisms. In collaboration with our partners, our group has assembled the genome of *P. polysora* and analyzed transcriptome sequences during the infection process. As a result, we have predicted 107 candidate effectors. Using the transient expression system of *Nicotiana benthamiana*, we have identified 8 effectors that clearly suppress plant immune responses. Based on these findings, our research team aims to identify the target proteins of these effectors in maize and elucidate the molecular mechanisms by which effectors

manipulate host targets to facilitate the infection of *P. polysora*.

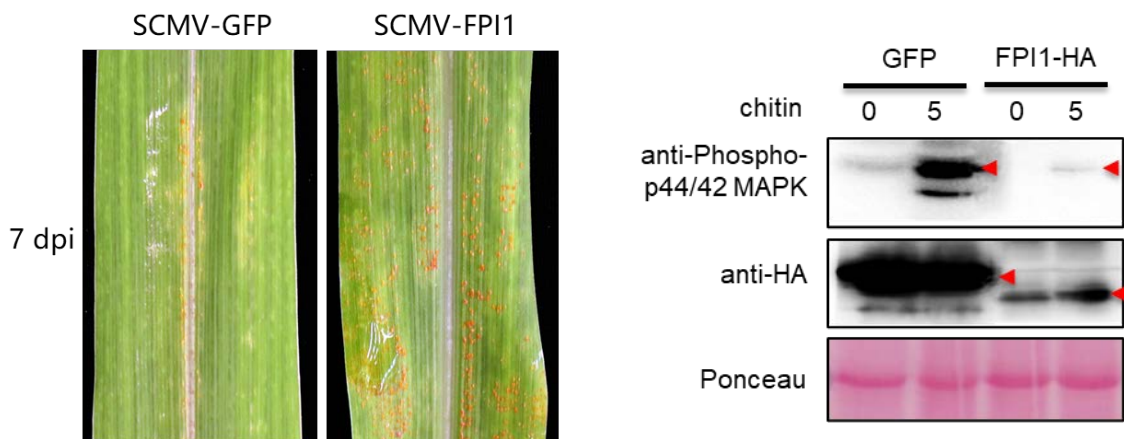


图1、效应蛋白FPI1抑制免疫响应，促进南方锈菌侵染。
Figure 1. The effector protein FPI1 suppresses immune responses and promotes *Puccinia polysora* infection.

2、玉米抗南方锈病的分子机制

挖掘抗病基因并培育抗病品种是病害绿色防控的重要策略。目前，已有的玉米南方锈病抗病基因数量较少。本课题组通过收集玉米材料，筛选出 25 个表现出高度抗南方锈病的品种，并构建了多个遗传群体，完成了 BSA 测序。在此基础上，我们定位了抗病基因，并结合分子生物学和生化手段解析了抗病蛋白的作用机制。本研究的成果将为抗多堆柄锈菌提供宝贵的玉米材料和基因资源，推动玉米抗病育种的进程。

Cloning Southern Corn Rust Resistant Genes

The identification of disease-resistant genes and the development of resistant varieties are key strategies for the green control of plant diseases. Currently, only a few resistance genes against maize southern rust are available. In this study, our team collected maize materials and identified 25 varieties exhibiting high resistance to southern rust. Multiple genetic populations were constructed, and BSA sequencing was performed. Based on this, we localized the resistance genes and used molecular biology and biochemical methods to analyze the mechanisms of resistance proteins. The results of this study will provide valuable maize materials and genetic resources for resistance to *Puccinia polysora* and accelerate the progress of maize disease resistance breeding.

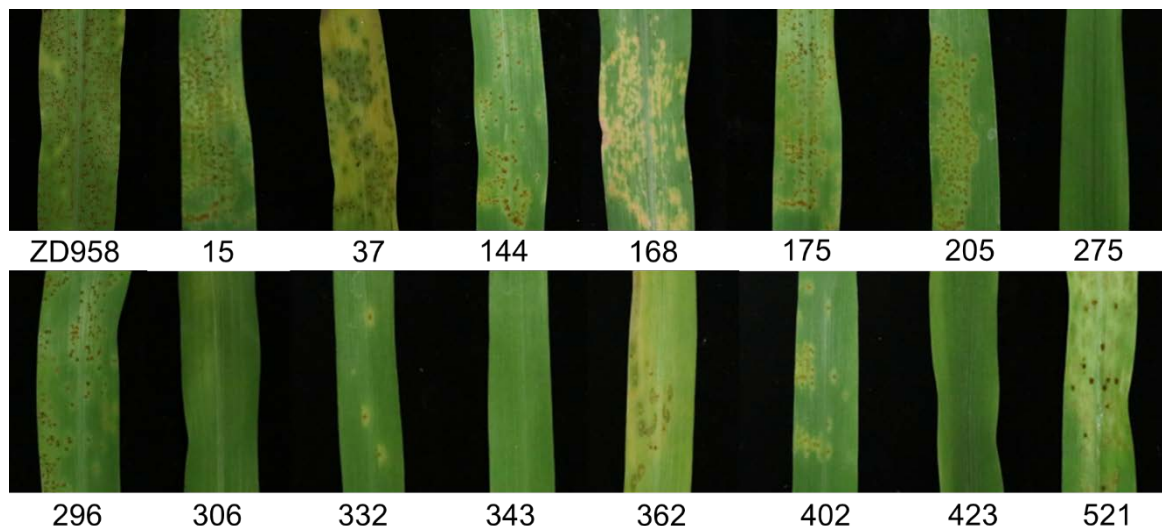


图2、玉米对南方锈菌的抗病性分析。

Figure 2. Resistance analysis of maize materials to southern corn rust.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

Ma M[#], Wang P[#], Chen R[#], Bai M, He Z, Xiao D, Xu G, Wu H., Zhou J, Dou D, Bi G, Liang X* (2024)
The OX11 kinase regulates plant immunity by linking microbial pattern-induced ROS burst to MAPK
activation. *Plant Cell* 37(1): koae311.

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梁鹏博，青年研究员。
研究方向：豆科植物-根瘤菌共生固氮分子机制。

(一) 研究进展

1、共生固氮中根瘤菌胞内侵染机制及其在非豆科作物中的工程化潜力挖掘

植物通过特定的细胞动力学来应对微生物的入侵。以豆科植物根毛中的感染为例，这些植物具备特定形态结构，能够捕获共生体，尤其是通过细胞骨架辅助形成侵染室，从而促进根瘤菌的胞内进入。然而，目前宿主如何调控这种细胞形态动态仍不清楚。我们的研究揭示了 **Formin** 家族蛋白 **INFO** 在根毛侵染中的细胞微丝组装中扮演着不可或缺的角色，这一点对于豆科植物中根瘤菌的胞内感染至关重要。**INFO** 与共生特异性的重膜纳米域在质膜上形成凝聚体，促进了所需的细胞微丝组装，以便共生体能够顺利进入宿主细胞。值得注意的是，**INFO** 的进化并不局限于共生固氮的特定谱系，而是普遍存在于更古老的丛枝菌根共生植物中。我们的研究还在苜蓿及非豆类作物番茄中验证了 **INFO** 在 **AM** 真菌胞内感染中的生物学功能。此外，我们意外发现宿主特有的共生转录因子 **NIN** 可以激活来源于番茄的 **INFO**，显示出非豆类植物中对根瘤菌响应特征的进化保留。我们的研究成果深入了对共生关系分子对话的理解，并提出了工程化框架：通过利用共生共享信号通路中的关键基因，可对非豆科作物中的生物固氮进行工程化潜力挖掘 (Qiao and Sun et al., in preparation)。

Evolutionarily Conserved Formin Proteins Facilitate Intracellular Symbiotic Microbe Infections in Legume and Non-Legume Plants

Plants deploy specific cell-surface-cytokinetic to counteract the invasion of intricate microbes. Like legume root hair infections own specific morphological inventions that entrap the symbiont, particularly an invaginated foci aided by cytoskeleton for rhizobia intracellular entry. How hosts manipulate this cellular morpho-dynamics remains largely unknown. Our investigations uncovered actin nucleating formin protein, termed **INFO**, as indispensable for the fragmented actin assembly, which is also essential for the intracellular infection by rhizobia in the model legume species *Medicago truncatula*. **INFO** condensates with the symbiotic-specific remorin nanodomains at the plasma membrane, facilitating the actin assembly required for symbiont entry. Given that **INFO** is evolutionarily not exclusive to the nodulating lineage but well confined among the more ancient symbiosis Arbuscular Mycorrhiza-forming species, its parallel function in **AM** fungi intracellular infection is then substantiated in both *Medicago* and non-legume crop tomato *Solanum*

lycopersicum. Additionally, the core root nodule symbiosis transcription factor NIN, unexpectedly, can activate the tomato-derived INFO, evidencing evolutionary retention of rhizobia-responsive signature in non-legume. Our findings bolster understanding of the molecular dialogues underpinning symbiotic associations and propose a framework in which non-legume nitrogen fixation likely could be engineered by leveraging genes from the common symbiosis signaling toolkit, more likely residing within their promoters (Qiao and Sun et al., in preparation).

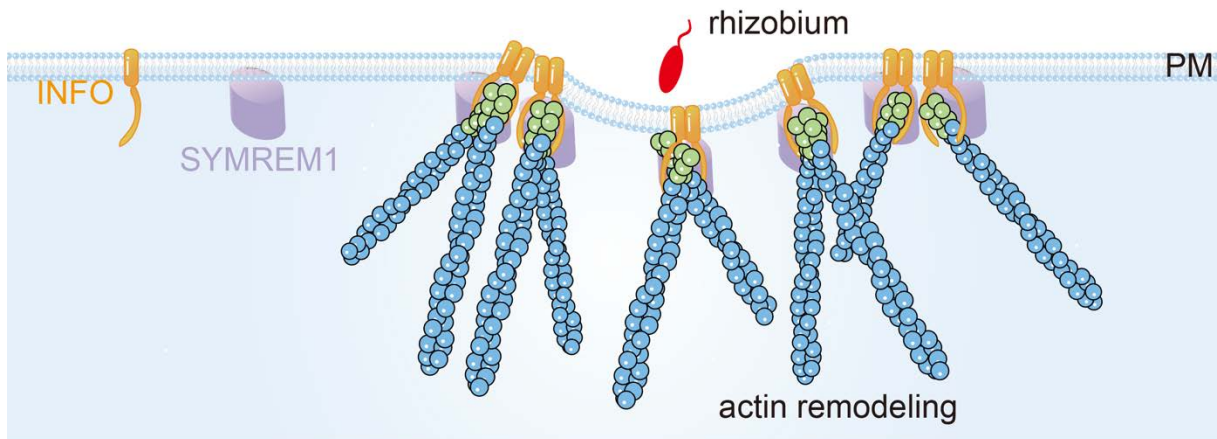


图1、INFO介导的根瘤菌侵染分子机制模型。

Figure 1. Molecular mechanism model of rhizobial intracellular infection mediated by INFO.

2、综述了豆科植物对根际氮浓度响应的共生固氮信号转导机制

利用共生微生物为植物提供养分，是在作物生产中实现全球碳中和的有效手段。然而，完全依赖微生物是不现实的，目前化肥的使用仍然是获得持续高产的必要条件。长期以来，人们了解到豆科植物和固氮根瘤菌之间的共生关系会受到氮的抑制。这是因为这种共生关系是互惠的，并且与植物的环境响应密切相关，其分子机制尚未完全理解。

梁鹏博团队和日本筑波大学 Takuya Suzuki 团队受邀联合撰写综述，概述了根际氮浓度-根瘤细胞内金属离子浓度-功能性根瘤”的分子调控模式，及其在现代农业中的高效固氮豆科植物改良的巨大潜力。此外，锌调控转录因子的聚集状态对分子生物学的基础研究推进具有重要的意义。论文围绕以下四部分进行了综述和展望：1. 植物 NLP 响应硝酸盐高浓度的硝酸盐抑制共生的多个关键步骤，加速根瘤的衰老。2. FUN 响应硝酸盐，促进根瘤衰老为了解析根瘤中硝酸盐响应机制；3. 第二信使锌通过 FUN 参与根瘤固氮的调；4. 未来展望：锌对转录因子的调控机制值得更加深入广泛的研究 (Qiao et al., *Nat Plants*, 2024)。

Zinc Sensing in Nodules Regulates Symbiotic Nitrogen Fixation

Utilizing symbiotic microorganisms to provide nutrients to plants is an effective means of achieving global carbon neutrality in crop production. However, relying entirely on microorganisms is unrealistic, and the use of chemical fertilizers remains a necessary condition for sustainable high yields. For a long time, it has been understood that the symbiotic relationship between leguminous plants and nitrogen-fixing root nodule bacteria is subject to nitrogen inhibition. This is because this symbiotic relationship is mutualistic and closely related to the plant's environmental responses, and its molecular mechanisms are not yet fully understood. Plants constantly adjust their gene expression and metabolism to thrive in diverse environments. In legume root nodules, the surprising role of zinc as an intracellular messenger links environmental changes to transcriptional control (Qiao et al., *Nat Plants*, 2024).

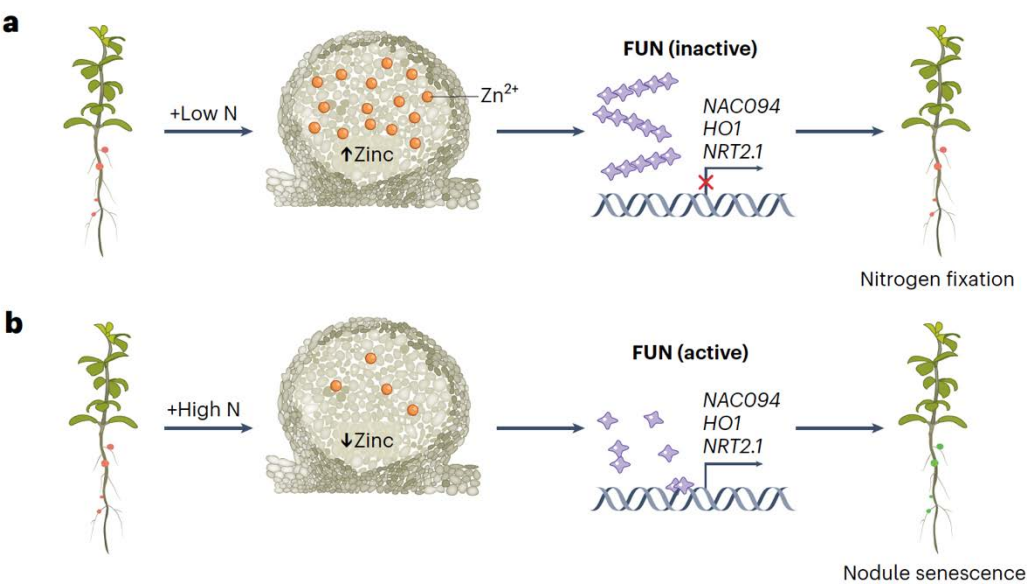


图2、FUN介导的结瘤性调控模型。

Figure 2. Model of FUN-mediated zinc sensing in the regulation of nodule functionality.

3、综述了几丁质介导的大豆根际共生菌和孢囊线虫的拮抗分子机制

植物的根际栖息着多样化的微生物，这些微生物可以作为寄生病原体存在，也可以与宿主形成共生关系。根结线虫(SCN)是一种严重的寄生虫，对全球大豆生产构成了重大威胁。在美国，仅根结线虫就导致了平均每年约 15 亿美元的产量损失。田间调查和温室研究表明，根结线虫造成的一个有害影响是对氮固定根瘤菌的结瘤以及菌根真菌的定殖产生拮抗作用，而这两者都是满足植物营养需求，特别是氮和磷的关键微生物共生体。然而，导致这种拮抗作用的分子机制仍不清楚。近期中国农业科学院植物保护研究所杨青团队发现孢囊线虫释放的几丁质酶是大豆根瘤共生和丛枝菌根共生能力的关键。

梁鹏博团队与美国俄克拉荷马州立大学的 Feng Feng 团队受邀联合撰写一篇评述性观点文章。文章从根际共生和免疫的角度切入，阐释了根结线虫(SCN)在根际通过“几丁质之战”拮抗植物-微生物共生互动的机制。文章的共生部分主要围绕大豆与根瘤菌、大豆与丛枝菌根菌之间的共生关系展开，并展望了基于蛋白结构的小分子设计在未来农业中的广阔应用前景 (Zhang et al., *Trends Microbiol*, 2024)。

Chitinase-Assistedwinner: Nematodesantagonize Symbioticmicrobes

The rhizosphere of plants harbors a diverse array of microorganisms, which can exist as parasitic pathogens or form symbiotic relationships with their hosts. The soybean cyst nematode (SCN) is a serious parasite that poses a significant threat to global soybean production. In the United States alone, SCN causes an estimated average annual yield loss of about \$1.5 billion. Field investigations and greenhouse studies have shown that one of the detrimental effects of SCN is its antagonistic action against the nodulation of nitrogen-fixing root nodule bacteria and the colonization of mycorrhizal fungi, both of which are key microbial symbionts that meet the nutritional needs of plants, particularly for nitrogen and phosphorus. However, the molecular mechanisms underlying this antagonism remain unclear. Recently, a team led by Yang Qing at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, discovered that chitinase released by cyst nematodes is crucial for soybean root nodule symbiosis and arbuscular mycorrhizal symbiotic capacity (Zhang et al., *Trends Microbiol*, 2024).

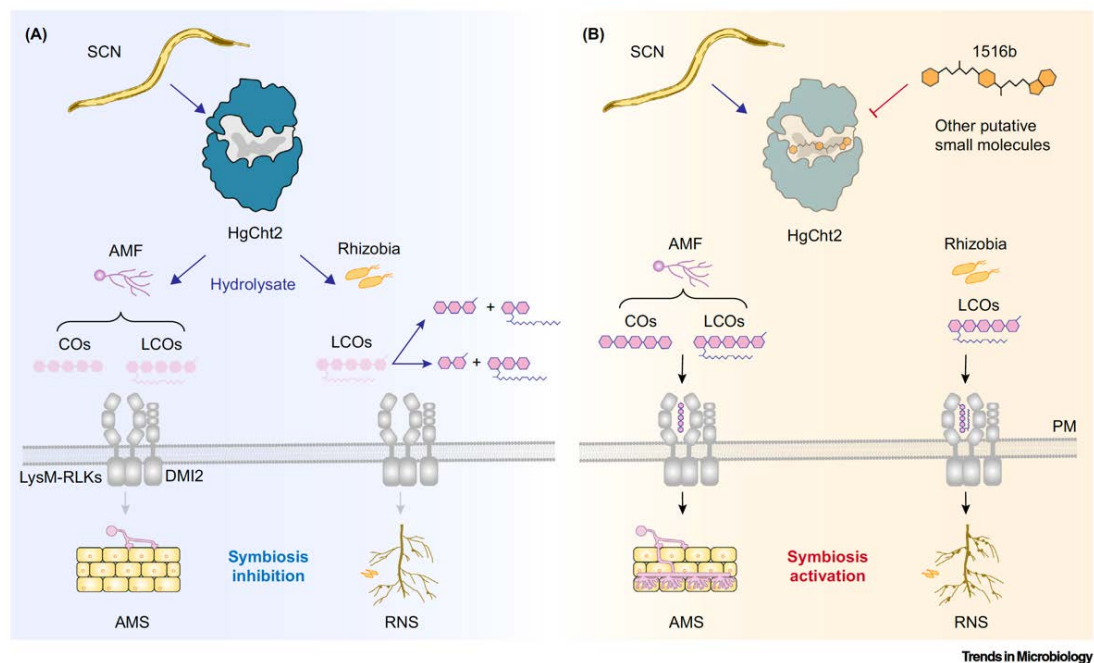


图 3、线虫几丁质酶介导的共生抑制和激活及其基于蛋白结构基础进行小分子设计示意图。

Figure 3. Schematic illustration of the inhibition and activation of symbiosis mediated by nematode chitinase and its structure-based inhibitor design.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Qiao L, Suzaki T, Liang P* (2024) Zinc sensing in nodules regulates symbiotic nitrogen fixation. **Nat Plants** 10(8): 1153-1154.
2. Zhang J, Sun H, Feng F, Liang P* (2024) Chitinase-assisted winner: nematodes antagonize symbiotic microbes. **Trends Microbiol** 32(10): 931-933.

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研究方向：植物免疫和逆境响应机制。

(一) 研究进展

TIR 抗病蛋白通过 NAD^+/ATP 诱导形成凝聚体激活免疫的分子机制

TIR 结构域是一个动物、植物和微生物都保守的免疫蛋白。植物除了编码全长 NLR 抗病蛋白，还编码了只含有 TIR 结构域的免疫蛋白。尤其在单子叶植物，如水稻、小麦、玉米，没有经典的 TIR-NLR，只编码了 TIR 结构域蛋白。TIR 结构域蛋白不仅能像 TIR-NLR 一样介导病原菌效应因子诱发免疫(ETI)，还可能参与模式识别受体介导的病原菌相关分子模式诱发免疫(PTI)。然而，TIR 结构域蛋白作为最小免疫模块，因缺少病原菌效应因子识别结构域和诱导寡聚的模块，其激活机制仍不清楚。我们研究发现，TIR 结构域抗病蛋白在底物 NAD^+/ATP 作用下形成凝聚体，激活 TIR 抗病蛋白的 NADase 酶活，从而产生免疫小分子激活植物 ETI 免疫反应。研究首次揭示了 TIR 结构域作为最小免疫模块通过形成凝聚体激活的新模式。该模式与 TIR-NLR 蛋白直接结合病原菌效应因子形成抗病小体激活的模式有本质的不同。TIR 结构域蛋白通过底物 NAD^+/ATP 结合诱导 BB-loop 构象改变，引起 TIR 自身寡聚化形成凝聚体，组装全酶催化中心，从而激活植物免疫反应。这种病原菌效应因子非依赖的自主激活特性，赋予了 TIR 结构域蛋白广泛参与多种免疫过程(ETI、PTI)的能力。同时也为解析单子叶作物，水稻、小麦、玉米里的 TIR 结构域抗病蛋白激活免疫提供了重要线索 (Song et al., *Nature*, 2024)。

Substrate-Induced Condensation Activates Plant TIR Domain Proteins

Plant nucleotide-binding leucine-rich repeat (NLR) immune receptors with an N-terminal Toll/interleukin-1 receptor (TIR) domain mediate recognition of strain-specific pathogen effectors, typically via their C-terminal ligand-sensing domains¹. Effector binding enables TIR-encoded enzymatic activities that are required for TIR NLR (TNL)-mediated immunity. Many truncated TNL proteins lack effector-sensing domains but retain similar enzymatic and immune activities. The mechanism underlying the activation of these TIR domain proteins remain unclear. Here we show that binding of the TIR substrates NAD^+ and ATP induces phase separation of TIR domain proteins in vitro. A similar condensation occurs with a TIR domain protein expressed via its native promoter in response to pathogen inoculation in planta. The formation of TIR condensates is mediated by



conserved self-association interfaces and a predicted intrinsically disordered loop region of TIRs. Mutations that disrupt TIR condensates impair the cell death activity of TIR domain proteins. Our data reveal phase separation as a mechanism for the activation of TIR domain proteins and provide insight into substrate-induced autonomous activation of TIR signalling to confer plant immunity (Song et al., *Nature*, 2024).

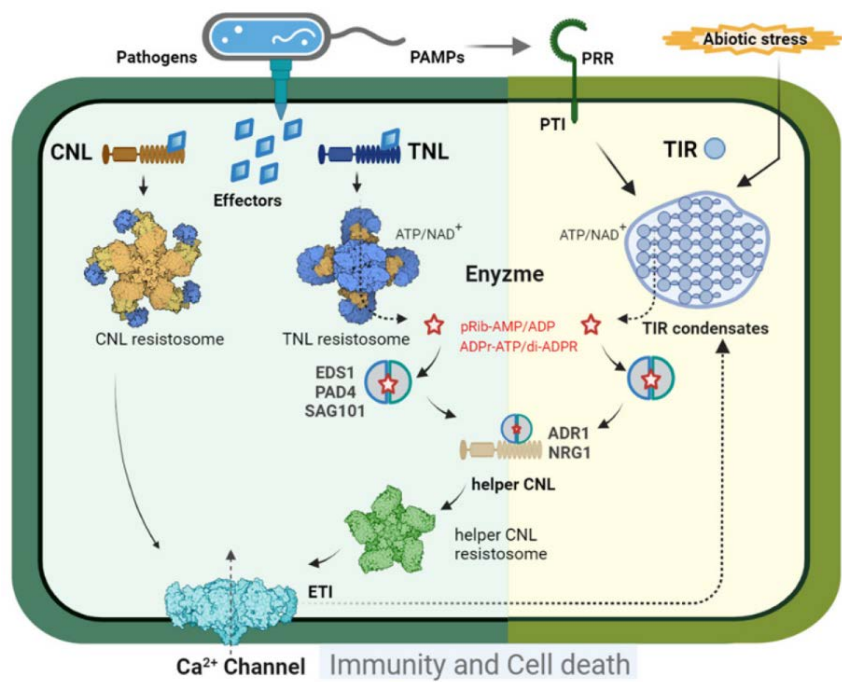


图1、植物TIR抗病蛋白激活免疫的分子机制。

Figure 1. The molecular mechanism of TIR-triggered immunity in *Arabidopsis*.

(二) 研究成果

发表论文：(*Corresponding author; #These authors contributed equally)

Song W[#], Liu L[#], Yu D, Bernard H, Jirschitzka J, Hang S, Jia A, Jemleniak W, Acker J, Laessle H, Wang J, Shen Q, Chen W, Li P, Parker J, Han Z, Schulze-Lefert P*, Chai J* (2024) Substrate-induced condensation activates plant TIR domain proteins. *Nature* 627: 847–853.

(三) 研究队伍

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马亮，青年研究员。

课题组

研究方向：植物抗盐碱分子机制研究。

(一) 研究进展

1、综述植物协同响应遮荫和环境胁迫的分子机制研究进展

近年来关于植物协同响应遮荫和环境胁迫分子机制的研究进展，主要从三个方面进行了系统性总结：1) 植物感知和适应遮荫信号的关键调控组分及信号转导通路；2) 植物协同响应遮荫和非生物胁迫(包括盐、干旱、水淹、土壤养分缺乏和极端温度等)的分子机制；3) 植物协同响应遮荫和生物胁迫(包括病原体和害虫)的分子策略。该论文还提出了该领域亟待研究的重要科学问题 (Han and Ma et al., *Plant J*, 2024)。

Molecular Mechanisms Underlying Coordinated Responses of Plants to Shade and Environmental Stresses

Shade avoidance syndrome (SAS) is triggered by a low ratio of red (R) to far-red (FR) light (R/FR ratio), which is caused by neighbor detection and/or canopy shade. In order to compete for the limited light, plants elongate hypocotyls and petioles by deactivating phytochrome B (phyB), a major R light photoreceptor, thus releasing its inhibition of the growth-promoting transcription factors PHYTOCHROME-INTERACTING FACTORS. Under natural conditions, plants must cope with abiotic stresses such as drought, soil salinity, and extreme temperatures, and biotic stresses such as pathogens and pests. Plants have evolved sophisticated mechanisms to simultaneously deal with multiple environmental stresses. In this review, we will summarize recent major advances in our understanding of how plants coordinately respond to shade and environmental stresses, and will also discuss the important questions for future research. A deep understanding of how plants synergistically respond to shade together with abiotic and biotic stresses will facilitate the design and breeding of new crop varieties with enhanced tolerance to high-density planting and environmental stresses (Han and Ma et al., *Plant J*, 2024).

2、一氧化氮促进种子萌发分子机制研究

一氧化氮 (nitric oxide, NO) 是生物体内一种重要的气体信号分子，参与调控植物的开花、种子萌发、生殖发育、器官发育、胁迫反应等众多生物学过程。虽然 NO 在调控植物种子萌发的过程早



有报道，但其如何通过抑制种子休眠，促进种子萌发的机制尚不清楚。我们的研究揭示了 NO 通过翻译后修饰调控 MYB30，使其结合 ABA 代谢酶 CYP707A2 启动子激活其转录，从而降低休眠种子中脱落酸(ABA)含量的积累，最终起始种子萌发的新机制 (Zhao et al., *Plant Cell.*, 2024)。

S-Nitrosylation of the Transcription Factor MYB30 Facilitates Nitric Oxide–Promoted Seed Germination in *Arabidopsis*

The gaseous signaling molecule nitric oxide (NO) plays an important role in breaking seed dormancy. NO induces a decrease in abscisic acid (ABA) content by transcriptionally activating its catabolic enzyme, the ABA 8-hydroxylase CYP707A2. However, the underlying mechanism of this process remains unclear. Here, we report that the transcription factor MYB30 plays a critical role in NO-induced seed germination in *Arabidopsis*. NO induces S-nitrosylation at Cys-49 of MYB30 and enhances its transcriptional activity. Conversely, the ABA receptors PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR) interact with MYB30 and repress its transcriptional activity. ABA promotes the interaction between PYL4 and MYB30, whereas S-nitrosylation releases the PYL4-mediated inhibition of MYB30 by interfering with the PYL4-MYB30 interaction. Our findings reveal that S-nitrosylation of MYB30 precisely regulates the balance of seed dormancy and germination, providing insights into the underlying mechanism of NO-promoted seed germination (Zhao et al., *Plant Cell.*, 2024).

3、番茄果实糖积累调控新机制

糖含量是影响番茄口感的重要因素，大多数消费者更喜欢偏甜的番茄。然而，因为糖含量与果实大小呈负相关，产量和品质是一个矛盾，现有番茄商业品种、尤其是大果番茄中糖含量普遍偏低。因此，如何在保障不影响番茄产量的前提下，培育美味的番茄品种是各国育种家努力追求的目标。该研究通过全基因组关联分析鉴定到一个抑制果实糖积累的刹车基因 *CDPK27* 及其同源基因 *CDPK26*，通过基因编辑两个基因，可使番茄果实糖含量增加高达 30%，且不影响单果重和单株产量，该发现阐明了果实糖积累的调控机制，为解决番茄育种中兼顾品质和产量的难题提供了新思路 (Zhang et al., *Nature*, 2024)。

Releasing A Sugar Brake Generates Sweeter Tomato Without Yield Penalty

In tomato, sugar content is highly correlated with consumer preferences, with most consumers preferring sweeter fruit. However, the sugar content of commercial varieties is generally low, as it is inversely correlated with fruit size, and growers prioritize yield over favour quality. Here we identified two genes, calcium-dependent protein kinase 27 (*SICDPK27*; also known as *SICPK27*) and its paralogue *SICDPK26*, that control fruit sugar content. They act as sugar brakes by phosphorylating a sucrose synthase, which promotes degradation of the sucrose synthase. Gene-edited *SICDPK27* and *SICDPK26* knockouts increased glucose and fructose contents by up to 30%, enhancing perceived sweetness without fruit weight or yield penalty. Although there are fewer, lighter seeds in the mutants, they exhibit normal germination. Together, these findings provide



insight into the regulatory mechanisms controlling fruit sugar accumulation in tomato and offer opportunities to increase sugar content in large-fruited cultivars without sacrificing size and yield (Zhang, et al., *Nature*, 2024).

(二) 研究成果

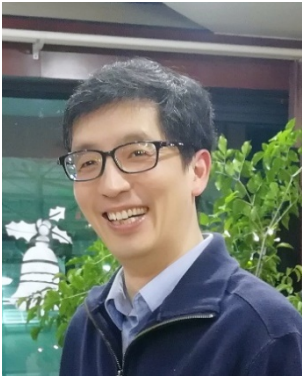
发表论文: (*Corresponding author; #These authors contributed equally)

1. Han R[#], Ma L[#], Terzaghi W, Guo Y, and Li J (2024) Molecular mechanisms underlying coordinated responses of plants to shade and environmental stresses. *Plant J* 117: 1893-1913.
1. Zhao H, Ma L, Shen J, Zhou H*, Zheng Y* (2024) S-nitrosylation of the transcription factor MYB30 facilitates nitric oxide-promoted seed germination in *Arabidopsis*. *Plant Cell* 36: 367-382.
2. Zhang J[#], Lyu H[#], Chen, J[#], Cao X, Du R, Ma L, Wang N, Zhu Z, Rao J, Wang J, Zhong K, Lyu Y, Wang Y, Lin T, Zhou Y, Zhou Y, Zhu G, Fei Z, Klee H, Huang S (2024) Releasing a sugar brake generates sweeter tomato without yield penalty. *Nature* 635: 647-656.

(三) 研究队伍

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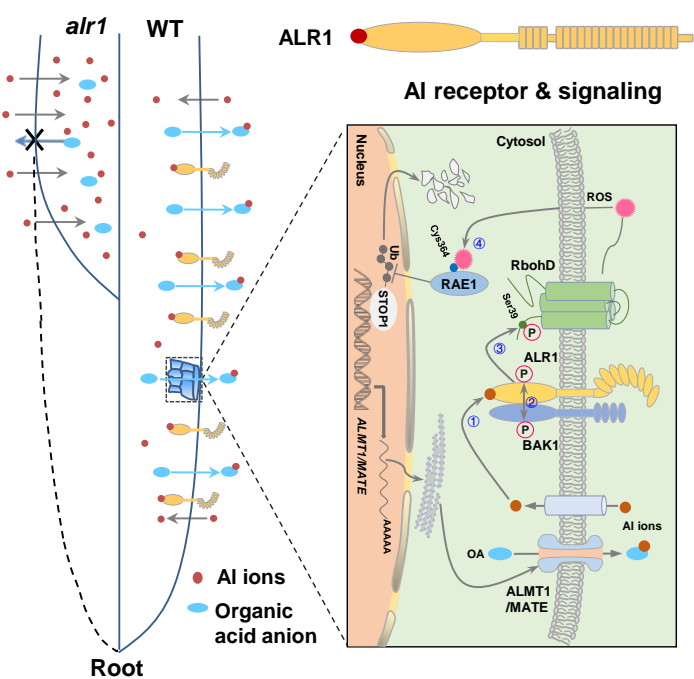
郑绍建，教授。教育部重大人才工程特聘教授(2009)，国家杰出青年科学基金获得者(2006)。

研究方向：
植物响应营养逆境的分子生理机制。

(一) 研究进展

1、植物铝离子感知及其信号转导的分子机制

铝毒害是酸性土壤上限制作物生产的主要因素之一，也是酸沉降导致森林退化的重要原因。尽管植物抗铝研究已进行了数十年，然而植物如何感知铝离子进而启动抗铝反应这个根本性的问题一直都没有解决。我们的研究首次回答了这个问题。我们筛选到一个对铝超敏感的类型受体激酶突变体 *aluminum resistance 1-1 (alr1-1)*，并系统证明了ALR1是一个铝离子受体。我们发现ALR1可以结合铝离子并感知其浓度变化，铝离子的结合可以促使ALR1招募共受体BAK1，进而促进ALR1对NADPH氧化酶RbohD Ser39位点的磷酸化，从而增强活性氧ROS的产生。ROS随后通过氧化修饰F-box蛋白RAE1，抑制后者对核心转录因子STOP1的泛素化降解，从而促进STOP1的蛋白累积，进而激活下游ALMT1、MATE等关键抗铝基因的表达，促进根系有机酸的分泌，最终提高植物的抗铝性(图1)。我们的研究解析了从铝离子感知到下游抗铝反应启动的完整信号通路，在植物铝胁迫研究领域具有里程碑的意义。这些研究也为生物体的离子感知机制提供了新的见解，也为今后抗酸铝作物和树木的分子育种提供重要理论依据(Ding et al., *Cell Res*, 2024)。



Molecular Mechanism of Aluminum Ion Sensing and Signaling in Plant

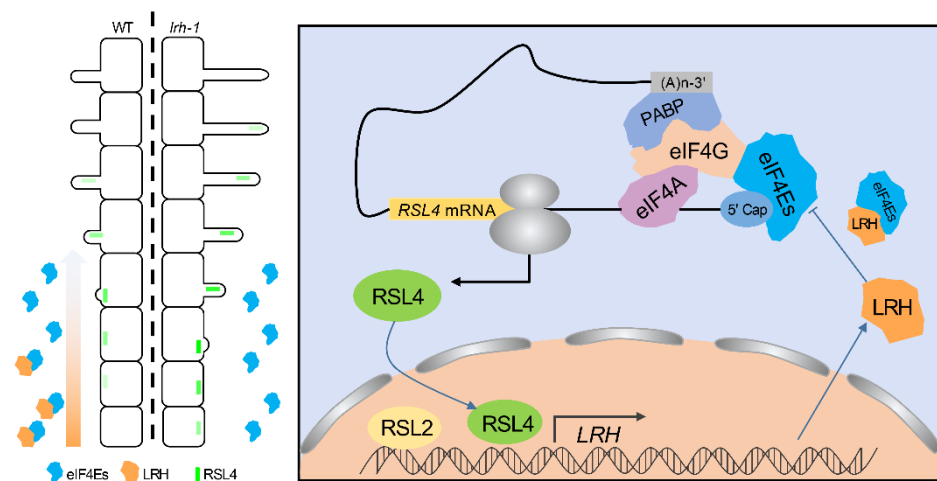
Aluminum (Al) toxicity is one of the main factor limiting crop production on acidic soils, and also the important factor of forest degradation caused by acid deposition. Although the research of plant Al resistance has been carried out for decades, the fundamental question of how plants sense

Al ions and in turn initiate Al resistance responses remains unknown. Our study has provided the answer to this question. Here we found an *Arabidopsis* mutant hypersensitive to Al. The gene encoding a leucine-rich-repeat receptor-like kinase, was named *Aluminum Resistance1* (*ALR1*). We demonstrated that *ALR1* is an Al ion receptor that senses its varying concentration. Al ions binding to *ALR1* cytoplasmic domain recruits *BAK1* co-receptor kinase and promotes *ALR1*-dependent phosphorylation of the NADPH oxidase *RbohD*, thereby enhancing reactive oxygen species (ROS) generation. ROS in turn oxidatively modify the *RAE1* F-box protein to inhibit *RAE1*-dependent proteolysis of the central regulator *STOP1*, thus activating organic acid anion secretion to detoxify Al (Figure 1). Our discovery of the entire pathway linking Al sensing to organic acid secretion is a major milestone in Al research, providing novel insights into ion-sensing mechanisms in living organisms, and enabling future molecular breeding of acid-soil-tolerant crops and trees, with huge potential for enhancing both global food security and forest restoration (Ding et al., *Cell Res*, 2023).

2、LRH-RSL4 反馈调节环调控根毛有限生长的分子机制

根毛是植物根系特化的表皮细胞所形成的管状凸起，对根系从土壤中获取水分和营养至关重要。尽管如此，根毛的生长却是有限的，这种有限生长如何受到精确调控目前还不清楚。我们的研究揭示了GYF结构域蛋白LONG ROOT HAIR(LRH)是一个全新的根毛抑制因子。LRH在根尖伸长区的根毛细胞中存在偏好性表达，并且其蛋白水平随着根毛发育呈梯度降低，与根毛伸长核心转录因子RSL4的蛋白累积呈现负相关。我们发现LRH通过与翻译起始因子eIF4Es互作抑制后者与RSL4 mRNA 5'帽子的结合，从而抑制RSL4的翻译，进而抑制根毛的伸长。同时，RSL4可以直接转录激活LRH的表达，从而

维持LRH在根毛细胞中的蛋白丰度，形成一条反馈调控回路(图2)。这种调控模式对根毛的伸长产生时空上的精确调节，为根毛的有限生长机制提供了新的见解 (Cui et al., *Curr Biol*, 2024)。



Molecular Mechanism of LRH-RSL4 Feedback Regulatory Loop in Control of the Determinant Growth of Root Hairs

Root hairs are tubular-shaped outgrowths of epidermal cells essential for plants acquiring

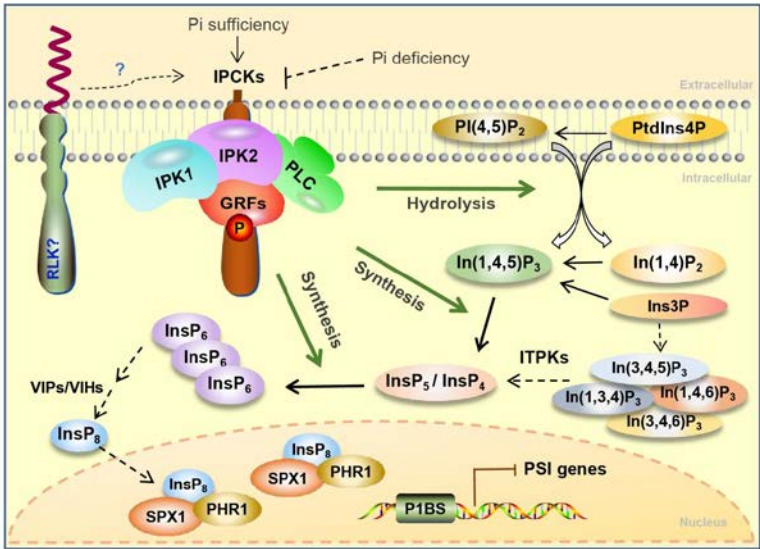


water and nutrients from the soil. Despite their importance, the growth of root hairs is finite. How this determinate growth is precisely regulated remains largely unknown. Here we identify LONG ROOT HAIR (LRH), a GYF domain-containing protein, as a unique repressor of root hair growth. LRH is preferentially expressed in the root hair cells in the root elongation zone, with its protein levels decreased gradiently during root hair development, and is negatively correlated with the protein accumulation of ROOT HAIR DEFECTIVE6-LIKE4 (RSL4), the master transcription factor of root hair elongation. We show that LRH inhibits the association of eukaryotic translation initiation factor 4Es (eIF4Es) with the 5' cap of RSL4 mRNAs, repressing RSL4 translation and thus root hair elongation. RSL4 in turn directly transactivates LRH expression to maintain a proper LRH gradient in the trichoblasts (Figure 2). Our findings reveal a previously uncharacterized LRH-RSL4 feedback regulatory loop that limits root hair growth, shedding new light on the mechanism underlying the determinate growth of root hairs (Cui et al., *Curr Biol*, 2024).

3、植物磷酸肌醇 InsP6 生物合成和磷稳态调控的新机制

六磷酸肌醇(又名植酸), 简称InsP6, 广泛存在于植物中, 是种子磷素的主要储存形式, 对植株体内磷稳态的维持具有重要作用, 同时又作为抗营养因子影响动物包括人体对营养成分的吸收和利用。因此, 培育低种子InsP6含量的农作物品种对改善作物营养品质和保护生态环境具有重要意义。但参与体内植酸合成的关键酶是如何被调控的仍不清楚。我们在短时间低磷处理后根系磷酸化蛋白组变化分析中发现了来自类受体胞质激酶RLCK V亚家族一个分支(命名为Inositol Polyphosphate-related Cytoplasmic Kinases 1-6, IPCK1-6)中的2个成员IPCK1和IPCK2的磷酸化水平快速受到外部磷缺乏的抑制, 将其中5个成员共突变后(六突致死), 种子中的InsP6含量下降达到75%, 说明IPCKs在调控种子和植株体内InsP6的含量和磷稳态中发挥着重要的功能。通过大量的生理、生化、分子、遗传等方法, 该研究最终揭示了IPCKs在调控InsP6生物合成的功能机制: 一方面IPCKs通过磷酸化

14-3-3蛋白(GRFs)促进其与IPK1、IPK2α/β和PI-PLCs等InsP6关键合酶的互作, 进而提高这些酶的活性; 另一方面, IPCKs发挥了类似支架蛋白的作用, 将这些酶招募到细胞质膜上形成蛋白复合体, 从而组装成一个高效的InsP6生物合成模块。这种调控模式对种子胚胎发育具有重要的生物学意义。该研究揭示了真核生物中InsP6生物合成的一种新机制, 也为培育低植酸种



子的作物新品种提供了潜在的新基因资源和理论依据; 同时也揭示了IPCKs作为一种重要的信号枢



组蛋白介导了细胞外磷信号调控胞内磷稳态的作用机制，深化和拓展了对现有植物磷信号转导的认知 (Xu et al., *Nat Commun*, 2024)。

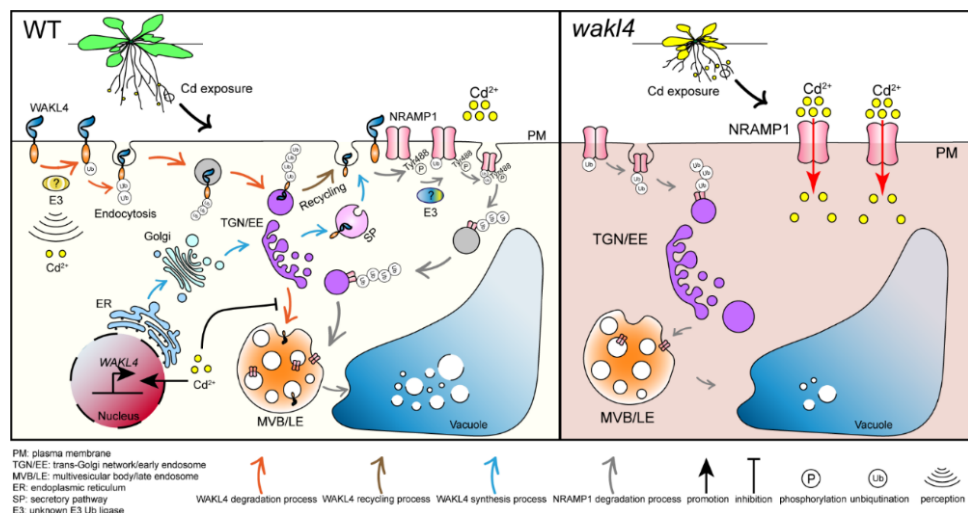
Aclade of Receptor-Like Cytoplasmic Kinases and 14-3-3 Proteins Coordinate Inositol Hexaphosphate Accumulation

Inositol hexaphosphate (InsP6) is the major storage form of phosphorus in seeds. Reducing seed InsP6 content is a breeding objective in agriculture, as InsP6 negatively impacts animal nutrition and the environment. Nevertheless, how InsP6 accumulation is regulated remains largely unknown. Here, we identify a clade of receptor-like cytoplasmic kinases (RLCKs), named Inositol Polyphosphate-related Cytoplasmic Kinases 1-6 (IPCK1-IPCK6), deeply involved in InsP6 accumulation. The InsP6 concentration is dramatically reduced in seeds of *ipck* quadruple (*T-4m/C-4m*) and quintuple (*C-5m*) mutants, accompanied with the obviously increase of phosphate (Pi) concentration. The plasma membrane-localized IPCKs recruit IPK1 involved in InsP6 synthesis, and facilitate its binding and activity via phosphorylation of GRF 14-3-3 proteins. IPCKs also recruit IPK2s and PI-PLCs required for InsP4/InsP5 and InsP3 biosynthesis respectively, to form a potential IPCK-GRF-PLC-IPK2-IPK1 complex. Our findings therefore uncover a regulatory mechanism of InsP6 accumulation governed by IPCKs, shedding light on the mechanisms of InsP biosynthesis in eukaryotes (Xu et al., *Nat Commun*, 2024).

4、类受体激酶 WAKL4 介导的植物主动降低镉累积的新机制

镉(Cd)是一种十分有害的重金属元素，以其较高的移动性和较强的生物毒性著称，严重威胁生态环境和人类健康。减少植物源性食物中Cd的积累对维护人类健康至关重要，但关于植物是否具有主动感知和响应环境中的Cd并减少其吸收和累积的能力仍不清楚。我们在对类受体激酶突变体库进行耐镉性筛选时发现WAKL4功能缺失后对镉的敏感性增加。通过大量的生理、生化、分子、遗传等方法，揭示了WAKL4调控植物Cd吸收的功能机制：Cd胁迫通过促进WAKL4基因的转录和抑制其蛋白降解，以快速诱导WAKL4蛋白在细胞质膜上的累积，进而磷酸化NRAMP1 Tyr488并促使NRAMP1进行内吞和液泡靶向降解，最终减少植物对Cd的吸收和积累。有意思的是，Col-0生态型在应对镉胁迫时，WAKL4-NRAMP1调控模块的功能很好地补偿了该生态型中行使将镉转运进入液泡解毒的HMA3的缺陷，并赋予了Col-0通过主动降低镉累积，从而提高其对镉的耐性的

WAKL4-NRAMP1 调控模块的功能很好地补偿了该生态型中行使将镉转运进入液泡解毒的HMA3的缺陷，并赋予了Col-0通过主动降低镉累积，从而提高其对镉的耐性的





能力。综上，由WAKL4-NRAMP1组成的信号调节模块赋予了植物有效且专一地限制过量Cd吸收和积累的能力，为植物Cd胁迫响应研究领域提供了新的见解，同时也为培育低Cd作物品种提供了潜在的新基因资源和理论依据 (Yuan et al., *Nat Commun*, 2024)。

The *Arabidopsis* Receptor-Like Kinase WAKL4 Limits Cadmium Uptake via Phosphorylation and Degradation of NRAMP1 Transporter

Cadmium (Cd) is a detrimental heavy metal propagated from soil to the food chain via plants, posing a great risk to human health upon consumption. Despite the understanding of Cd tolerance mechanisms in plants, whether and how plants actively respond to Cd and in turn restrict its uptake and accumulation remain elusive. Here, we identify a cell wall-associated receptor-like kinase 4 (WAKL4) involved in specific tolerance to Cd stress. We show that Cd rapidly and exclusively induces WAKL4 accumulation by promoting WAKL4 transcription and blocking its vacuole-dependent proteolysis in roots. The accumulated WAKL4 next interacts with and phosphorylates the Cd transporter NRAMP1 at Tyr488, leading to the enhanced ubiquitination and vacuole-dependent degradation of NRAMP1, and consequently reducing Cd uptake. Our findings therefore uncover a mechanism conferred by the WAKL4-NRAMP1 module that enables plants to actively respond to Cd and limit its uptake, informing the future molecular breeding of low Cd accumulated crops or vegetables (Yuan et al., *Nat Commun*, 2024).

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

2. Ding Z[#], Xu C[#], Yan J, Wang Y, Cui M, Yuan J, Wang Y, Li G, Wu J, Wu Y, Xu J, Li C, Shi Y, Mao C, Guo J, Zhou J, Benhamed M, Harberd NP, Zheng S* (2024) The LRR receptor-like kinase ALR1 is a plant aluminum ion sensor. **Cell Res** 34: 281-294.
3. Xu L, Cui M, Xu C, Zhang M, Li G, Xu J, Wu X, Ding W, Mao C, Benhamed M, Ding Z*, Zheng S* (2024) A clade of receptor-like cytoplasmic kinases and 14-3-3 proteins coordinate inositol hexaphosphate accumulation. **Nat Commun** 15: 5107.
4. Yuan J, Zhao Y, Yu S, Sun Y, Li G, Yan J, Xu J, Ding W, Benhamed M, Qiu R, Zheng S, Ding Z* (2024) The *Arabidopsis* receptor-like kinase WAKL4 limits cadmium uptake via phosphorylation and degradation of NRAMP1 transporter. **Nat Commun** 15: 9537.
5. Cui M, Xu C, Wang T, Zhao L, Wang Y, Li G, Yan J, Xu J, Liu R, Wag Z, Harberd NP, Zheng S, Ding Z* (2024) An LRH-RSL4 feedback regulatory loop controls the determinate growth of root hairs in *Arabidopsis*. **Curr Biol** 34: 313-326.
6. Tian W, Cai W, Zhu C, Kong Y, Cao X, Zhu L, Ye J*, Zhang J*, Zheng S* (2024) STOP1 regulates CCX1-mediated Ca²⁺ homeostasis for plant adaptation to Ca²⁺ deprivation. **J Integr**



- Plant Biol** 66: 2126-2139.
7. Li Y, Ren M, Wu Y, Wang L, Liu Y, Zhu J, Xu J, Mo X, Wu Z, Wu P, Lu C, Zheng S, Mao C* (2024) A root system architecture regulator modulates OsPIN2 polar localization in rice. **Nat Commun** accepted.
 8. Zhu Q, Ren M, Jiang Y, He C, Ding Z, Zheng S, Wang Z, Jin C* (2024) Co-mutation of OsLPR1/3/4/5 provides a promising strategy to minimize Cd contamination in rice grains. **J Hazard Mater** 476: 135165.
 9. Xu L, Jia W, Tao X, Ye F, Zhang Y, Ding Z, Zheng S, Qiao S, Su N, Wu S, Guo J* (2024) Structures and mechanisms of the *Arabidopsis* cytokinin transporter AZG1. **Nat Plants** 10: 180-191.
 10. Wang J, Luo Y, Ding Z, Zheng S, Qiao S, Wang Y, Guo J, Yang W, Su N* (2024) Structures and ion transport mechanisms of plant high-affinity potassium transporters. **Mol Plant** 17: 409-422.
 11. An J, Brik Chaouche R, Pereyra-Bistraín LI, Zalzalé H, Wang Q, Huang Y, He X, Dias Lopes C, Antunez-Sanchez J, Bergounioux C, Boulogne C, Dupas C, Gillet C, Pérez-Pérez JM, Mathieu O, Bouché N, Fragkostefanakis S, Zhang Y, Zheng S, Crespi M, Mahfouz M, Ariel F, Gutierrez-Marcos J, Raynaud C, Latrasse D, Benhamed M* (2024) An atlas of the tomato epigenome reveals that KRYPTONITE shapes TAD-like boundaries through the control of H3K9ac distribution. **Proc Natl Acad Sci USA** 121(28):e2400737121.
 12. He X, Dias Lopes C, Pereyra-Bistraín LI, Huang Y, An J, Chaouche RB, Zalzalé H, Wang Q, Ma X, Antunez-Sanchez J, Bergounioux C, Piquerez S, Fragkostefanakis S, Zhang Y, Zheng S, Crespi M, Mahfouz M, Mathieu O, Ariel F, Gutierrez-Marcos J, Li XW, Bouché N, Raynaud C, Latrasse D, Benhamed M* (2024) Genetic-epigenetic interplay in the determination of plant 3D genome organization. **Nucleic Acids Res** 52(17):10220-10234.

(三) 研究队伍

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**寿惠霞****寿惠霞，教授。****课题组****研究方向：植物营养生理与分子生物学。**

(一) 研究进展

1、大豆多组学数据库 SoyOD 的构建与应用

目前，大豆基因组学研究已积累了数千种大豆种质资源的遗传变异信息及其他多维组学数据，但现有数据库未能及时整合完整的数据集，限制了大豆研究的数据利用效率。本团队开发的大豆多组学数据库 SoyOD，涵盖了大豆的基因组学、遗传学及相关数据，为大豆功能基因挖掘提供了直观且用户友好的界面，构建了交互式在线工具包，形成了一站式服务平台，旨在助力大豆生物学的深入研究。本研究全面收集并整合了多个大豆基因组、转录组、重测序和表型等数据，并采用了多种分析方法，对数据进行细致的解析和加工。在源头数据方面，我们共完成 940 份大豆种质资源的深度测序；完成各类种质资源 162 组种子发育期的转录组测序；完成种质资源 53 类表型数据的测定及 2500 多幅表型图片的拍摄；在此基础上，我们搭建了一个综合性的大豆多组学数据库 SoyOD，整合了基因组、转录组和群体遗传信息，为研究人员提供了一个高效的平台，用于查询基因组信息、基因表达数据和遗传变异等；通过引入了多个交互式工具，包括基因 ID 转换、基因组坐标转换、序列提取、热图和 JBrowse 浏览等，增强了数据库的功能性和实用性。该研究成果于 2024 年 11 月在《*Genomics, Proteomics & Bioinformatics*》上发表，相关数据库网站为公众开放：<https://bis.zju.edu.cn/soyod>。

SoyOD: An Integrated Soybean Multi-omics Database for Mining Genes and Biological Research

Soybean is a globally important crop for food, feed, oil, and nitrogen fixation. A variety of multi-omics studies has been carried out, generating datasets ranging from genotype to phenotype. In order to efficiently utilize these data for basic and applied research, a soybean multi-omics database with extensive data coverage and comprehensive data analysis tools was established. The Soybean Omics Database (SoyOD) integrates important new datasets with existing public datasets to form the most comprehensive collection of soybean multi-omics information. Compared to existing soybean databases, SoyOD incorporates an extensive collection of novel data derived from the deep-sequencing of 984 germplasms, 162 novel transcriptome datasets from seeds at different developmental stages, 53 phenotypic datasets, and more than 2500 phenotypic images.



In addition, SoyOD integrates existing data resources, including 59 assembled genomes, genetic variation data from 3904 soybean accessions, 225 sets of phenotypic data, and 1097 transcriptomic sequences covering 507 different tissues and treatment conditions. Moreover, SoyOD can be used to mine candidate genes for important agronomic traits, as shown in a case study on plant height. Additionally, powerful analytical and easy-to-use toolkits enable users to easily access the available multi-omics datasets, and to rapidly search genotypic and phenotypic data in a particular germplasm. The novelty, comprehensiveness, and userfriendly features of SoyOD make it a valuable resource for soybean molecular breeding and biological research. SoyOD is publicly accessible at <https://bis.zju.edu.cn/soyod>.

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Li J, Ni Q, He G, Huang J, Chao H, Li S, Chen M, Hu G, Whelan J, Shou H* (2024) SoyOD: An Integrated Soybean Multi-omics Database for Mining Genes and Biological Research. **Genom Proteom Bioinf** 13:qzae080. DOI: 10.1093/gpbjnl/qzae080.
2. Liao W, Guo R, Qian K, Shi W, Whelan J, Shou H* (2024) The acyl-acyl carrier protein thioesterases GmFATA1 and GmFATA2 are essential for fatty acid accumulation and growth in soybean. **Plant J** 118(3):823-838.
3. Zhu J, Li J, Hu X, Wang J, Fang J, Wang S, Shou H* (2024) Role of OsbHLH156-OsIRO2 transcription factor complex in regulating manganese, copper and zinc transporters in rice. **J Exp Bot** 75(3): 1112-1127.
4. He CM, Shou H* (2024) PHO1: linking phosphate nutrition translocation and floral signalling in plants. **J Exp Bot** 75(16): 4693-4696.

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毛传澡
课题组

毛传澡，教授。

研究方向：(1) 磷高效吸收利用的分子机理；(2) 养分高效根构型的分子调控机制。

(一) 研究进展

1. 揭示了 SNARE 蛋白介导水稻中生长素转运体的胞内转运及根系形态建成

根的形态建成对幼苗的存活和植物生长至关重要。水稻作为主要粮食作物，具有典型的须根系。但其根系建成的分子机制尚不清晰。我们通过正向遗传学分析和图位克隆鉴定了调控水稻根形态建成的重要基因 *SYNTAXIN 132*(*OsSYP132*)，该基因的突变体 *srm1* 同时缺失不定根和侧根。研究发现 *srm1* 中 *OsSYP132* 发生了点突变产生提前终止密码子，导致 *OsSYP132* 丢失了跨膜后区域 (PTM)。基于体内 IP-LC-MS/MS、体外脂质体融合实验、蛋白结构预测和分子动力学模拟等实验，我们鉴定了功能性 SNARE 复合物 *OsSYP132*-*OsNPSN13*-*OsSYP71*-*OsVAMP721/722*，并发现 *OsSYP132* 的 PTM 区域的完整性对基于 *OsSYP132* 的 SNARE 复合物介导的囊泡与质膜的融合至关重要。通过生长素信号示踪标记及原位免疫实验等，我们发现 *srm1* 中 *OsPIN1b* 的胞内转运及其在 不定根和侧根原基细胞中的质膜定位发生了严重错乱，扰乱生长素的正常分布，无法建立生长素浓度梯度和顶端最大值，进而导致不定根及侧根原基在突破表皮前停止生长(图 1)。该研究阐明了水稻中基于 *OsSYP132* 的 SNARE 复合物在生长素分布和胚后根系发育中的作用，并拓展了我们对囊泡融合及其与水稻根形态发生的关系的认识。相关研究结果发表在 *New Phytologist* 上 (Zhu et al. 2024)。

Revealed SNARE Protein Mediating Intracellular Transport of Auxin Transporters and Root Morphogenesis in Rice.

Root morphogenesis is essential for seedling survival and plant growth. As a major grain crop, rice has a typical fibrous root system. However, the molecular mechanism of root formation is still unclear. We identified *SYNTAXIN 132* (*OsSYP132*), an important gene regulating rice root morphogenesis, through forward genetic analysis and map based cloning. The mutant of this gene *srm1* is lost both adventitious and lateral roots. We found that *OsSYP132* in *srm1* has a point mutation to produce an early mature stop codon, resulting in *OsSYP132* losing the post-transmembrane region (PTM). Based on in vivo IP-LC-MS/MS, in vitro liposome fusion experiments, protein structure prediction and molecular dynamics simulation, we identified the functional SNARE



complex OsSYP132-OsNPSN13-OsSYP71-OsVAMP721/722. The integrity of the PTM region of OsSYP132 was found to be critical for the fusion of OsSYP132 SNARE complex mediated vesicles with plasma membranes. Through auxin signaling marker line and in situ immunostaining, we found that the intracellular transport of OsPIN1b in *srm1* and its plasma membrane localization in adventitious root and lateral root primordial cells were seriously disturbed, disrupting the normal distribution of auxin and failing to establish auxin concentration gradient and apex auxin maximum. The adventitious roots and lateral root primordia then stop growing before breaking out the epidermis (Figure 1). This study elucidates the role of OsSYP132-based SNARE complex in auxin distribution and postembryonic root development in rice, and expands our understanding of vesicle fusion and its relationship with rice root morphogenesis. The related results were published in the *New Phytologist* (Zhu et al. 2024).

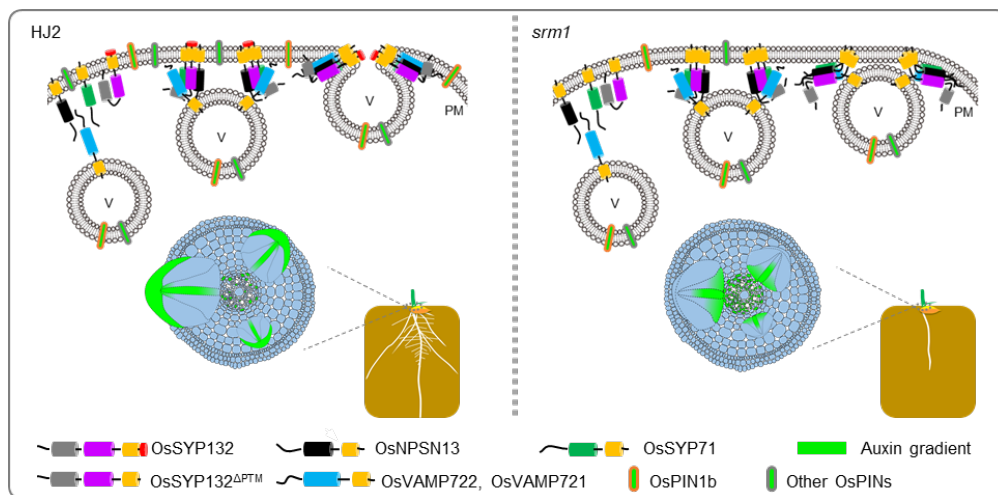


图 1、OsSYP132 在调控根系发育中作用的工作模型

Figure 1. Working model of OsSYP132 in regulating root development.

2、磷吸收调控及磷调控根构型的分子机制

克隆了调控水稻磷吸收利用的蛋白磷酸酶 PP5，明确其调控磷吸收的分子生理机制 (Wang et al., *Environ Exp Bot*, 2024)，揭示了活性氧参与调控水稻适应低磷的分子机制。详细综述了水稻根感知环境磷水平及根构型响应磷水平的分子机制研究进展，低磷条件下植物通过调控独角金内酯的合成影响根和地上部发育的机制,讨论了水稻养分高效根构型遗传改良的实践策略并提出了今后的研究方向 (Lu et al.; *Mol Plant*, 2024; Lu et al.; *Plant Physiol*, 2024)。

Molecular Regulation Mechanisms of Phosphorus Absorption and Root Architecture

We cloned and functionally identified protein phosphatase PP5 which regulates phosphorus uptake and utilization in rice (Wang et al., *Environ Exp Bot*, 2024), and revealed the molecular mechanism of reactive oxygen species (ROS) in rice adaptation to low phosphorus environment.



We reviewed the molecular mechanisms of rice root sensing and root architecture response to environmental phosphorus levels, the mechanism of strigolactone mediated plant root and aboveground development under low phosphorus conditions. Practical strategies for genetic improvement of nutrient-efficient root architecture in rice were discussed and future research directions were proposed (Lu et al.; *Mol Plant*, 2024; Lu et al.; *Plant Physiol*, 2024).

(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Li Y, Ren M, Wu Y, Wang L, Liu Y, Zhu J, Xu J, Mo X, Wu Z, Wu P, Lu C, Zheng S, Mao C* (2024) A root system architecture regulator modulates OsPIN2 polar localization in rice. **Nat Commun** accepted.
2. Lu H, Lin R, Deng M, Jin K, Mao C* (2024) New mechanistic insights into phosphate-starvation-regulated plant architecture change and nutrient uptake. **Mol Plant** 17 (1):19-21.
3. Zhu J, Li M, Lu H, Li Y, Ren M, Xu J, Ding W, Wang Y, Wu Y, Liu Y, Wu Z, Mo X, Mao C* (2024) The t-SNARE protein OsSYP132 is required for vesicle fusion and root morphogenesis in rice. **New Phytol** <https://doi.org/10.1111/nph.20180>.
4. Lu H, Ren M, Lin R, Jin K, Mao C* (2024) Developmental responses of roots to limited phosphate availability: Research progress and application in cereals. **Plant Physiol** DOI:10.1093/plphys/kiae495.
5. Wang F, Deng M, Wu K, Xu J, Liu Y, Wu Z, Mao C* (2024) Protein phosphatase 5 mediates plant growth and phosphate homeostasis in rice. **Environ Exp Bot** 219:105625.

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1. 毛传澡, 朱建树, 李梦真, 徐纪明, 吴运荣, 莫肖蓉; 水稻根形态建成调控基因 CLRD1 及其应用; 专利号: ZL 202210683006.8; 授权公告日: 2024 年 3 月 29 日。
2. Mao CZ, Meng FN, Xiang D, Wang AD; Root-secreted peptide PEP1 in rice and gene encoding the same and use thereof; 专利号: 17/780,930, 授权公告日: 2024 年 11 月 6 日。

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研究方向：植物适应环境温度升高的分子机理及耐高温作物的遗传基础与分子改良。

(一) 研究进展

1、水稻高温抗性的昼夜差异调控机制

OsGRP3/OsGRP162 的表达具有昼夜节律性和热诱导性，其表达水平在夜间达到峰值且在深夜强烈受高温诱导。热胁迫对 *OsGRP3/OsGRP162* 在午夜的节律性诱导很大程度上依赖于 EC 组分之一 *OsELF3-2*。通过基因编辑技术获得了 *grp3 grp162* 双突变体。在正常温度条件下，*grp3 grp162* 双突变体正常生长，而热胁迫下，*grp3 grp162* 双突变体苗期存活率和生殖期结实率均显著低于野生型(ZH11)对照。为了研究 *OsGRP3* 和 *OsGRP162* 是否参与水稻昼夜耐热性的调控，分别在白天和夜晚对野生型和 *grp3 grp162* 双突变体进行同样时长的热胁迫处理。结果发现，*OsGRP3* 和 *OsGRP162* 功能缺失后，*grp3 grp162* 双突变体生殖期高温夜晚处理后比白天处理后结实率和产量下降更为明显。对热胁迫下 ZH11 和 *grp3 grp162* 双突变体进行了转录组学分析，发现在热胁迫下 *grp3 grp162* 双突变体显示出热应激响应基因的诱导表达水平下降，并且以外显子跳跃为主的 mRNA 选择性剪接事件增加。进一步实验证明 *OsGRP3/OsGRP162* 能够直接结合靶标基因的 mRNA，与剪接体核心组分 U1 和 U2 SnRNPs 发生相互作用参与选择性剪接调控。综上所述，*OsGRP3* 和 *OsGRP162* 正向调控水稻耐热性。时钟基因 EC 尤其是 *ELF3-2* 在上游调控 *OsGRP3* 和 *OsGRP162* 的深夜节律性和热诱导型表达，而 *OsGRP3* 和 *OsGRP162* 直接结合下游靶标 RNA 并与剪接体组分互作参与 mRNA 选择性剪接调控，防止外显子跳跃等事件发生，保证热响应基因的正常功能，实现了对水稻耐热性的昼夜调控，更多地在深夜保护水稻免受高温伤害。

Diurnal Regulation of Alternative Splicing Associated With thermotolerance in Rice by Two Glycine-Rich RNA-Binding Proteins

Rice (*Oryza sativa* L.) production is threatened by global warming associated with extreme high temperatures, and rice heat sensitivity is differed when stress occurs between daytime and nighttime. However, the underlying molecular mechanism are largely unknown. We show here that two glycine-rich RNA binding proteins, *OsGRP3* and *OsGRP162*, are required for thermotolerance in rice, especially at nighttime. The rhythmic expression of *OsGRP3/OsGRP162* peaks at midnight, and at these coincident times, is increased by heat stress. This is largely dependent on the evening complex component *OsELF3-2*. We next found that the double mutant of *OsGRP3/OsGRP162* is



strikingly more sensitive to heat stress in terms of survival rate and seed setting rate when comparing to the wild-type plants. Interestingly, the defect in thermotolerance is more evident when heat stress occurred in nighttime than that in daytime. Upon heat stress, the double mutant of *OsGRP3/OsGRP162* displays globally reduced expression of heat-stress responsive genes, and increases of mRNA alternative splicing dominated by exon-skipping. This study thus reveals the important role of *OsGRP3/OsGRP162* in thermotolerance in rice, and unravels the mechanism on how *OsGRP3/OsGRP162* regulate thermotolerance in a diurnal manner.

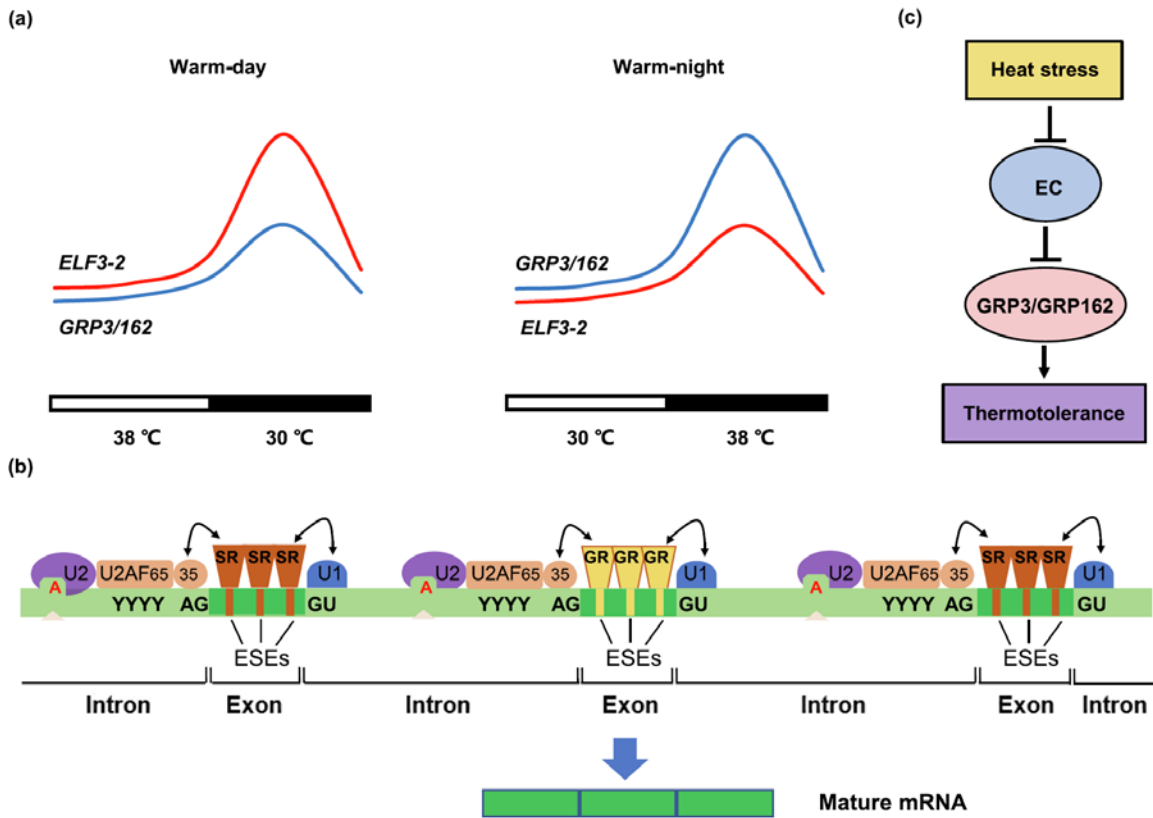


图 1、*OsGRP3* 和 *OsGRP162* 在昼夜耐热性中的作用的模型。(a)*OsELF3-2* 调控 *OsGRP3/OsGRP162* 的日间表达。在温暖的白天条件下，*OsGRP3/OsGRP162*(蓝线)的表达在午夜被 EC 抑制，因为 *OsELF3-2*(红线)在这个时间点高度表达。在温暖的夜晚条件下，热胁迫会下调 *OsELF3-2* 的表达，在午夜提高 *OsGRP3/OsGRP162* 的表达水平。(b)*OsGRP3/OsGRP162* 在热胁迫条件下防止外显子跳跃。富含丝氨酸(SR)的蛋白质与外显子剪接增强子(ESE)结合，并与 U1/U2 组分相互作用，促进 RNA 剪接并连接两个相邻的外显子，相比之下，富含甘氨酸(GR)的蛋白质 *OsGRP3/OsGRP162* 与 ESE 结合并与 U1/U2 组分相互作用，促进水稻在热胁迫条件下的外显子保留(防止外显子跳跃)。(c)*OsGRP3/OsGRP162* 对耐热性的昼夜调节。热胁迫有节律地下调 EC 成分之一 *OsELF3* 的表达，释放 EC 对 *OsGRP3/OsGRP162* 表达的抑制作用，导致 *OsGRP3/OsGRP162* 在午夜(ZT 18 小时)有节律地表达峰值，节律性地调控水稻耐热性。

Figure 1. Working models for the function of *OsGRP3* and *OsGRP162* in diurnal thermotolerance. (a) Diurnal expression of *OsGRP3/OsGRP162* regulated by *OsELF3-2*. Under warm day conditions, the expression of *OsGRP3/OsGRP162* (blue line) is largely suppressed by EC at midnight because *OsELF3-2* (red line) is highly



expressed at this timepoint. Under warm night conditions, the expression of OsELF3-2 is down-regulated by heat stress, lifting the expression level of OsGRP3/OsGRP162 at midnight. (b) Promoting exon inclusion by OsGRP3/OsGRP162 under heat stress conditions. Serine-rich (SR) proteins bind to exonic splicing enhancers (ESEs) and interact with U1/U2 components to stimulate RNA splicing and joining two adjacent exons, in contrast, glycine-rich (GR) proteins OsGRP3/OsGRP162 bind to ESEs and interact with U1/U2 components to promote exon inclusion (prevent exon skipping) in rice under heat stress conditions. (c) Diurnal regulation of thermotolerance by OsGRP3/OsGRP162. Heat stress rhythmically down-regulates the expression of OsELF3, one of the EC components, to release the inhibitory effect of EC on the expression of OsGRP3/OsGRP162, leading to rhythmical expression peak of OsGRP3/OsGRP162 at midnight (ZT 18 h) and diurnal thermotolerance in rice.

2、2OGD超家族的JOX基因负调控水稻耐旱性

植物激素在生长发育及抗逆方面发挥重要作用。2-oxoglutarate-dependent dioxygenase (2OGD) 超家族是在激素合成与代谢方面发挥重要作用。目前该家族在烟草等经济作物中还未被鉴定。我们利用生物信息学手段系统鉴定了烟草2OGD家族的126个成员,发现60个成员参与各种激素的合成与代谢。同时,我们还鉴定了它们的进化、表达和胁迫相应。

我们发现,2OGD家族的JOX亚分支的多个基因在干旱胁迫中被诱导表达。利用遗传学手段,我们在烟草和水稻中敲除JOX家族成员,发现敲除系能够增强植物的耐旱性。在水稻中,单独敲除OsJOX3和OsJOX4能提高水稻苗期耐旱性。进一步调查发现,敲除OsJOX3和OsJOX4提高了水稻的JA水平,POD等耐旱相关生理指标提高,水稻耐旱相关基因Os**bHLL148**和Os**JAUP1**的表达提高(图2)。这些数据为提高水稻耐旱性提供了新的线索 (Zhang et al., *Int J Biol Macromol.*, 2024)。

Genome-Wide Identification of Hormone Biosynthetic and Metabolism Genes in the 2OGD Family of Tobacco and JOX Genes Silencing Enhances Drought Tolerance in Plants

Phytohormones play crucial roles in regulation of plant growth and tolerance to abiotic stresses. The 2-oxoglutarate-dependent dioxygenase (2OGD) superfamily responds to hormone biosynthesis and metabolism in plants. However, the Nt2OGD family in tobacco has not been fully explored. In this study, we identify 126 members of the Nt2OGD family, and 60 of them are involved in hormone biosynthesis and metabolism process (Nt2OGD-Hs), including 1-aminocyclopropane-1-carboxylic acid oxidases (ACO), dioxygenases for auxin oxidation (DAO), gibberellin (GA) 20-oxidases and 3-oxidases (GA20ox and GA3ox), carbon-19 and carbon-20 GA 2-oxidases (C19-GA2ox and C20-GA2ox), lateral branching oxidoreductases (LBO), jasmonate-induced oxygenases (JOX), downy mildew resistant 6, and DMR6-like oxygenases (DMR6/DLO). Gene duplication analysis suggests the segmental duplication and whole genome duplication (WGD) might be a potential mechanism for the expansion of this family. Expression analysis reveals that most of Nt2OGD-Hs show tissue-specific expression patterns, and some of them respond to environmental conditions. Of Nt2OGD-Hs, the expression of *NtJOX3* and *NtJOX5*, which are involved in JA metabolism, exhibits remarkable changes during drought treatments. Silencing of



NtJOX3 or *NtJOX5* increases tobacco tolerance to drought stress. Furthermore, knocking out *OsJOX3* and *OsJOX4*, respectively in rice, result in high tolerance to drought. Taken together, our work comprehensively identifies the *Nt2OGD* family in tobacco and provides new insights into roles of the JA pathway in drought tolerance in plants.

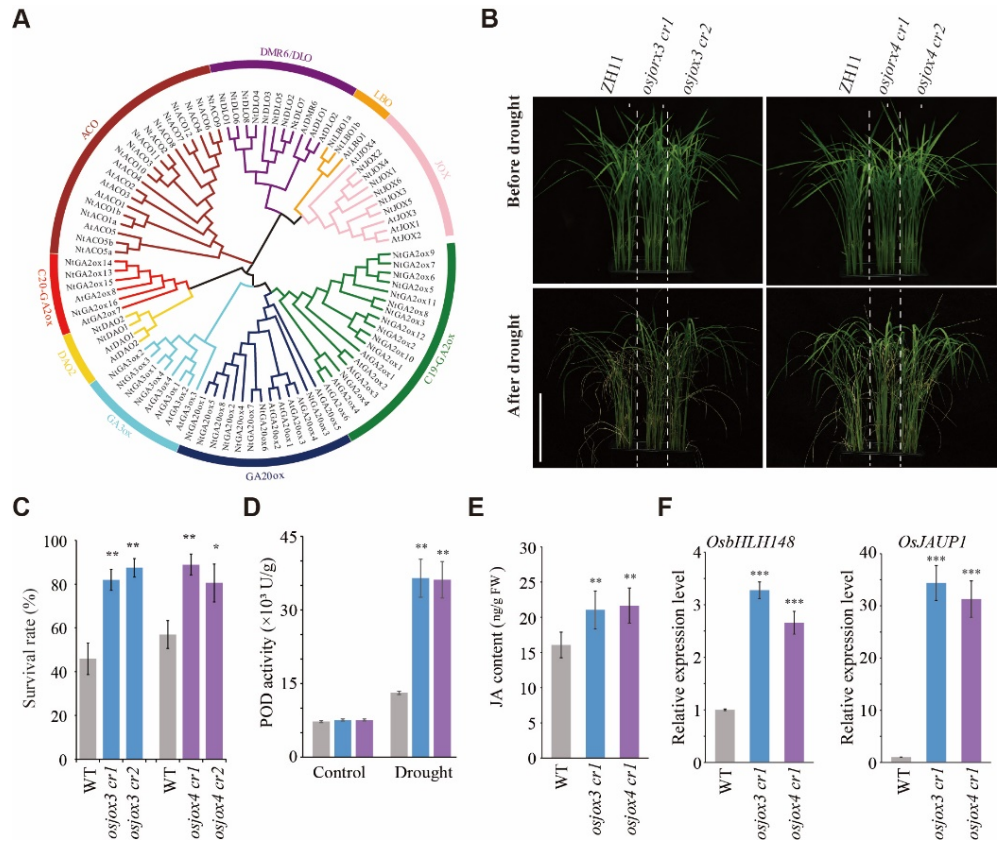


图2、敲除 *OsJOX3* 和 *OsJOX4* 提高水稻苗期耐旱性。

Figure 2. Knocking out *OsJOX3* and *OsJOX4* improves the drought tolerance in rice seedlings.

3、新基因SGSP10调控水稻粒型

粒型由粒长、粒宽和粒厚组成，是重要籽粒产量和外观品质性状。尽管很多粒型基因已被鉴定，但粒型与次生代谢之间的调控机制还知之甚少。我们克隆并鉴定了一个新的粒型调控基因 *SGSP10* (*SMALL GRAIN AND SHORT PANICLE 10*)。缺失 *SGSP10* 会导致水稻粒长变短、粒宽变宽。 *SGSP10* 编码一个在高等植物中保守、功能未知蛋白。通过生化手段，我们筛选到一个 *SGSP10* 互作蛋白 *OsMYB108*。 *OsMYB108* 已知调控苯丙烷-木质素代谢基因的表达，但它是否调控粒型还不清楚。我们发现，敲除 *OsMYB108* 导致粒长变长，粒宽变窄。进一步研究发现， *SGSP10* 与木质素和粒型正相关，而 *OsMYB108* 与木质素和粒型负相关。我们推测， *SGSP10* 可能负调控 *OsMYB108*，进而影响苯丙烷-木质素代谢，从而调控水稻粒型(图3)。 *SGSP10* 和 *OsMYB108* 均为调控水稻粒型的新基因，这些数据为水稻粒型改良提供了重要线索 (Liu et al., *J Genet Genomics*, 2024)。



The *SGSP10*-*Osmyb108* Module Controls Grain Size via Regulating the Lignin Accumulation in Rice

Grain size, which encompasses length, width and thickness, is a key agricultural trait determining both grain yield and appearance quality in rice. While many grain size regulators have been identified, the molecular mechanisms underlying grain size and the lignin content remain elusive. Here, we clone and characterize *SGSP10* (*SMALL GRAIN AND SHORT PANICLE 10*), a novel regulator controlling grain size in rice. Loss of function of *SGSP10* results in smaller grain size and shorter panicle length. *SGSP10* encodes an evolutionarily conserved protein with functions uncharacterized in higher plants. Biochemical assays reveal that *SGSP10* interacts with transcription factor *OsMYB108*, which acts as a negative regulator of the lignin biosynthesis. Knockout of *OsMYB108* results in longer and slender grain size, and higher lignin content, demonstrating that *OsMYB108* negatively regulates both grain size and the lignin content. The *sgsp10,osmyb108* double mutant partially rescues the *sgsp10* phenotype, indicating *SGSP10* may negatively regulate *OsMYB108* function to control grain size. Analysis of natural variations and haplotypes in *SGSP10* reveals that this locus is associated with grain size, suggesting an artificial selection on *SGSP10* during rice domestication. Together, our findings reveal a novel mechanism in the regulation of grain size and lignin metabolism, thus providing crucial insights for improving crop yields.

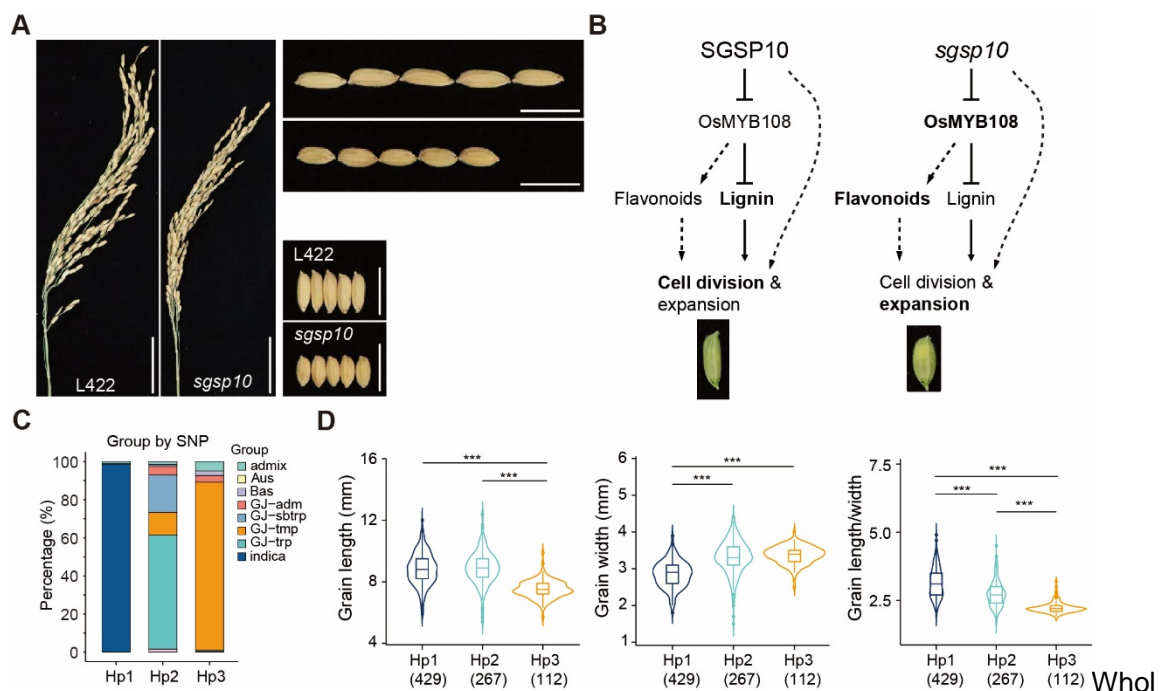


图3、*SGSP10*通过次生代谢调控水稻粒型。

Figure 3. *SGSP10* regulates rice grain size via modulating the secondary metabolism.



(二) 研究成果

发表论文: (*Corresponding author; #These authors contributed equally)

1. Yang C, Luo A, Lu H, Davis S, Liu J* (2024) Diurnal regulation of alternative splicing associated with thermotolerance in rice by two glycine-rich RNA-binding proteins. **Sci Bull** 69: 59-71.
2. Zhang L, Zhu Q, Sun J, Yao Z, Qing, T, Ma H, Liu J* (2024) XBAT31 regulates reproductive thermotolerance through controlling the accumulation of HSFB2a/B2b under heat stress conditions. **Cell Rep** 43(6): 114349.
3. Wang J, Gao J, Li W, Liu J* (2024) CCaP1/CCaP2/CCaP3 interact with plasma membrane H⁺-ATPases and promote thermo-responsive growth by regulating cell wall modification in *Arabidopsis*. **Plant Commun** 5(7): 100880.
4. Zhang L, Liu J* (2024) 3D chromatin reorganization during stress responses in plants. **Sci Bull** 69: 847-849.
5. Qing T, Xie T, Zhu Q, Lu H, Liu J* (2024) Regulation of metal homeostasis by two F-group bZIP transcription factors bZIP48 and bZIP50 in rice. **Plant Cell Environ** 47: 1852-1864.
6. Zhu Q, Zhang L, Liu J* (2024) NFXL1 functions as a transcriptional activator required for thermotolerance at reproductive stage in *Arabidopsis*. **J Integr Plant Biol** 66: 54-65.
7. Zhang R, Chen X, Wang Y, Hu X, Zhu Q, Yang L*, Zhou M* (2024) Genome-wide identification of hormone biosynthetic and metabolism genes in the 2OGD family of tobacco and JOX genes silencing enhances drought tolerance in plants. **Int J Biol Macromol** 280: 135731.
8. Zhang R, Xi X, Chen X, Wang Y, Zhou M* (2024) Comparing time-series transcriptomes between chilling-resistant and -susceptible rice reveals potential transcription factors responding to chilling stress. **Front Plant Sci** 15: 1451403.
9. Liu H, Ni J, Zhang Y, Chen Y, Luo Y, Wang Y, Shang F, Yang Y, Xu R, Cao L, Hong L, Xu J, Yang Y, Zhou M* (2024) The SGSP10-OsMYB108 module controls grain size via regulating the lignin accumulation in rice. **J Genet Genomics** revised.
10. Xu S, He X, Trinh D, Zhang X, Wu X, Qiu D, Zhou M, Xiang D, Roeder A, Hamant O*, Hong L* (2024) A 3-component module maintains sepal flatness 1 in *Arabidopsis*. **Cur Biol** 34: 4007-4020.
11. Felgines L, Rymer B, Martin L, Xu G, Matteoli C, Himber C, Zhou M, Eis J, Coruh C, Bohrer M, Kuhn L, Chicher J, Pandey V, Hammann P, Wohlschlegel J, Waltz F, Law J*, Blevins T* (2024) CLSY docking to Pol IV requires a conserved domain critical for small RNA biogenesis and transposon silencing. **Nat Commun** accepted.



12. Yan J, Feng Z, Xiao Y, Zhou M, Zhao X, Lin X, Shi W, Busch W, Li B* (2024) ANAC044 orchestrates mitochondrial stress signaling to trigger iron-induced stem cell death in root meristems. *Proc Natl Acad Sci USA* accepted.

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研究方向：植物生长发育及逆境适应分子信号调控。

(一) 研究进展

1、对 MPK4 在植物生长发育和免疫过程中的功能提出新见解

为了抵御病虫害等外界威胁，植物进化出复杂的免疫系统。然而，过度的免疫反应往往以牺牲植物生长为代价。理解植物生长发育与免疫之间的平衡调控机制一直是植物学研究的热点问题。丝裂原活化蛋白激酶(Mitogen-Activated Protein Kinase, MAPK)组成的级联是真核生物中高度保守的信号通路，调控多个关键植物生长发育过程，同时在植物免疫过程中发挥重要功能。拟南芥 MPK3/MPK6 级联以及 MPK4 级联是植物学研究中最受关注的两条 MAPK 信号通路。其中 MPK4 级联功能缺失突变体植物同时表现出严重的生长发育缺陷和持续激活的自身免疫等表型。多种表型混杂在一起，使得单纯利用传统 *mpk4* 突变体等作为主要研究材料去解析 MPK4 在特定生长发育或植物免疫过程中的功能及其机制十分困难。我们建立了一个条件型失活 *mpk4* 突变体研究体系，对 MPK4 在植物生长/发育和免疫过程中的功能提出了新见解。

通过定点突变改变激酶 ATP-binding pocket 的空间结构后，激酶的活性可被 ATP 结构类似物 NA-PP1 特异抑制，从而导致该激酶无法结合 ATP 而失去活性。利用该化学分子遗传学手段，研究人员成功建立了条件型 MPK4 活性缺失突变体 *MPK4SR* (SR: Sensitized-variant Rescued; 基因型: *P_{MPK4}:MPK4^{YG} mpk4*, 图 1)。通过一系列的生化以及植物体内实验，研究人员证明 NA-PP1 抑制剂可以特异并高效地抑制 MPK4^{YG} 变体(variant)的活性。因此可以在任意阶段处理正常生长发育的 *MPK4SR* 植物，使用 NA-PP1 即时关闭 MPK4 级联信号，进行不同条件下的表型观察等研究，这为分开研究 MPK4 在不同时空中的多个功能提供了可能。研究发现，在前期正常生长发育的植物中短期抑制 MPK4 信号通路不影响植物的抗病性，但随着对 MPK4 活性抑制的延长至 3 天左右，植物表现出生长停滞，同时对病原菌的抗性显著增强。转录组分析显示，MPK4 在调控植物多种基础生命过程(如有丝分裂、转录启动、细胞壁大分子分解)中发挥着至关重要的作用。此外，本研究发现 MPK4 持续弱激活的 *MPK4CA* 转基因植株表现出提前开花和叶片衰老的表型。*MPK4CA* 植物对病原菌抵抗力的降低与提前衰老的表型密切相关。这些结果进一步凸显了 MPK4 在植物生长发育调控中不可或缺的作用，同时表明 MPK4 在植物生长与免疫适应之间的微妙平衡中起着关键作用。本研究中 *MPK4SR* 体系为研究 MPK4 在植物生长发育与免疫的功能提供了全新的工具。研究者可以利用化学

试剂时空特异地即时有效抑制 MPK4 激酶活性，避免了传统突变体中因长期缺失 MPK4 活性导致的严重生长发育缺陷或者自身免疫等复杂表型对研究的干扰。因此可作为传统 T-DNA 插入 *mpk4* 突变体研究体系的重要补充 (Zhang et al., *Plant Physiol*)。

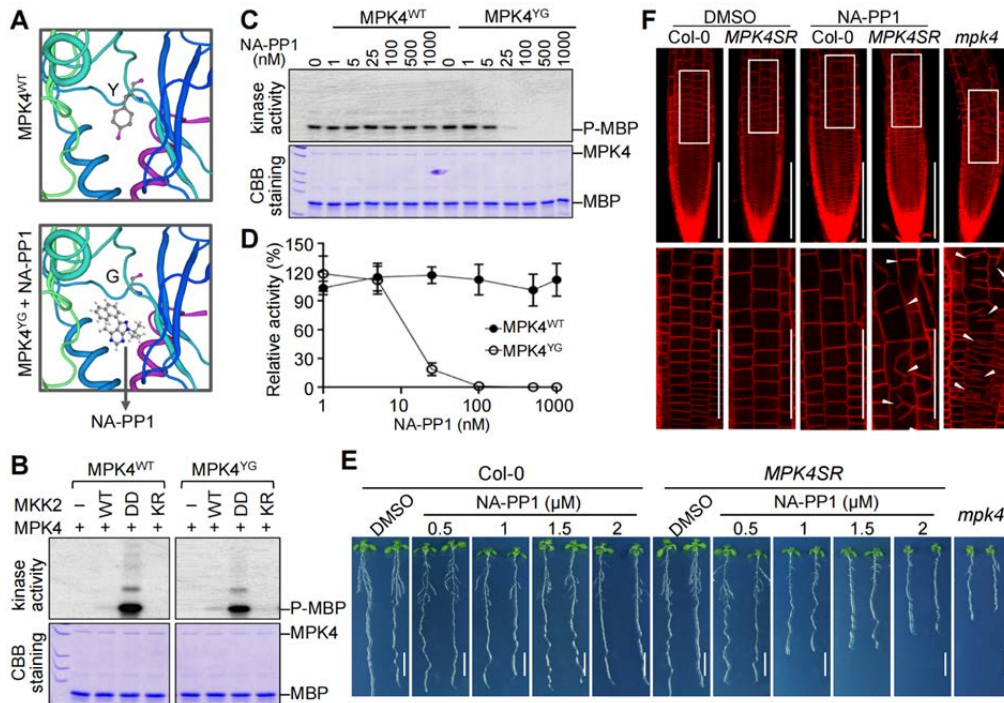


图 1、条件型 MPK4 活性缺失突变体 *MPK4SR* 的构建与验证。

Figure 1. Generation and validation of chemical-sensitized MPK4 variant-rescued *mpk4* system.

2、一个全新 ANAC106-DELLA 分子模块调控 GA 合成及信号的稳态影响花粉发育

我们课题组近年一直致力于 MPK3/MPK6 级联信号调控植物生长发育的机制研究。我们通过对 MPK3/MPK6 信号激活及关闭后的植株进行转录组分析并 RT-qPCR 验证,发现了一个 NAC 家族转录因子在 MPK3/MPK6 信号激活后其表达量显著上调。该转录因子在拟南芥基因组中的功能暂未得到注释,其编码的蛋白在 N 端有一段保守的 NAC 结构域, C 端为结构多变的转录激活结构域,符合 NAC 转录因子家族的特征。该转录因子未被收录在之前拟南芥中鉴定到的 105 个 NAC 转录因子之列,因此我们将其命名为 ANAC106。我们发现 35S:ANAC106 过表达转基因植株以及融合转录抑制结构域的 ANAC106-EAR 转基因植株均表现出花粉败育的表型。对不同发育时期花药切片观察发现花药绒毡层的降解在 35S:ANAC106 过表达植株中提前,而在 ANAC106-EAR 转基因植株中延迟,这两种情况均导致花粉败育。结合转录组以及 DAP-Seq 分析发现 ANAC106 直接靶向调控 GA 合成关键基因 *GA3ox2* 和 *GA3ox4* 的表达。已有研究表明, GA-DELLA 信号通路在调控花粉发育过程中发挥至关重要的作用, 外源施加 GA 或通过遗传学手段降低内源活性 GA 合成均会影响花粉发育, 同样 DELLA 蛋白的活性对于花粉正常发育也是必需的。通过超高效液相色谱串联质谱检测 ANAC106 不同转基因植株叶片中活性 GA 的含量发现, 在 35S:ANAC106 和 DEX 处理后



GVG:ANAC106 叶片中活性 GA 含量显著升高,而在 ANAC106-EAR 中略有降低。与此相应,在 35S:ANAC106 植株中两个核心的 DELLA 蛋白 RGA 和 GAI 的丰度显著降低,在 ANAC106-EAR 中显著积累。分别用绒毡层和花粉发育后期特异性表达启动子 *LTP12* 和 *LAT52* 驱动 RGA 回补到 35S:ANAC106 花药中可以显著恢复过表达植株的不育表型,以上遗传学证据表明 GA-DELLA 信号通路参与介导 ANAC106 调控花粉发育。有趣的是,我们还发现拟南芥五个 DELLA 蛋白中除了 RGL1 其余四个均可以和 ANAC106 互作,而这种互作会以浓度依赖的形式反馈抑制 ANAC106 的转录激活活性,这种反馈抑制保证了在正常发育情况下花药中活性 GA 维持在合适的水平,确保花粉的正常发育。不同发育时期各组织中内源 GA 水平的精细化时空调控对于确保植物正常生长发育至关重要,我们的研究鉴定到一个新的功能未注释的 NAC 转录因子 ANAC106 通过调控 GA 合成及信号的稳态影响花粉发育。该部分研究成果已于近日投稿至 *Nature Plants* 杂志。

A DELLA-ANAC106 Feedback Circuit Regulates Pollen Development by Modulating Gibberellin Metabolism and Signaling Homeostasis

Gibberellin (GA), one of the five classical plant hormones, plays a crucial role in pollen development. In this study, we identified a previously unknown NAC transcription factor, designated as ANAC106 (AT3G12910), which regulates pollen development through the GA-DELLA signaling pathway. Overexpression of ANAC106, as well as a dominant-negative variant ANAC106-EAR, resulted in severe pollen developmental defects and male sterility. Semi-thin section analysis revealed that the degradation of the tapetum layer occurred earlier in ANAC106-overexpressing (ANAC106-OE) plants and later in ANAC106-EAR plants compared to the wild-type Col-0. Integrative analysis of DAP-Seq and RNA-Seq data indicated that ANAC106 directly activates the expression of genes in GA biosynthesis pathway, including *GA3ox2* and *GA3ox4*. Associated with this, levels of bioactive GAs were elevated in ANAC106-OE plants and slightly reduced in ANAC106-EAR plants. As a result, the protein levels of RGA and GAI, two core DELLA proteins, were found to be decreased in ANAC106-OE plants and increased in ANAC106-EAR plants. Expressing the RGA protein under the control of the tapetum-specific promoter *LTP12* or the late pollen development-specific promoter *LAT52* greatly improved pollen viability in ANAC106-OE plants, providing genetic evidence that ANAC106 regulates pollen development via the GA-DELLA pathway. Meanwhile, we found that DELLA proteins inhibit the transcriptional activity of ANAC106 through physical interaction. Taken together, our findings establish DELLA-ANAC106 feedback loop as a critical determinant in modulating GA metabolism and signaling homeostasis, thereby coordinating tapetum and pollen development.

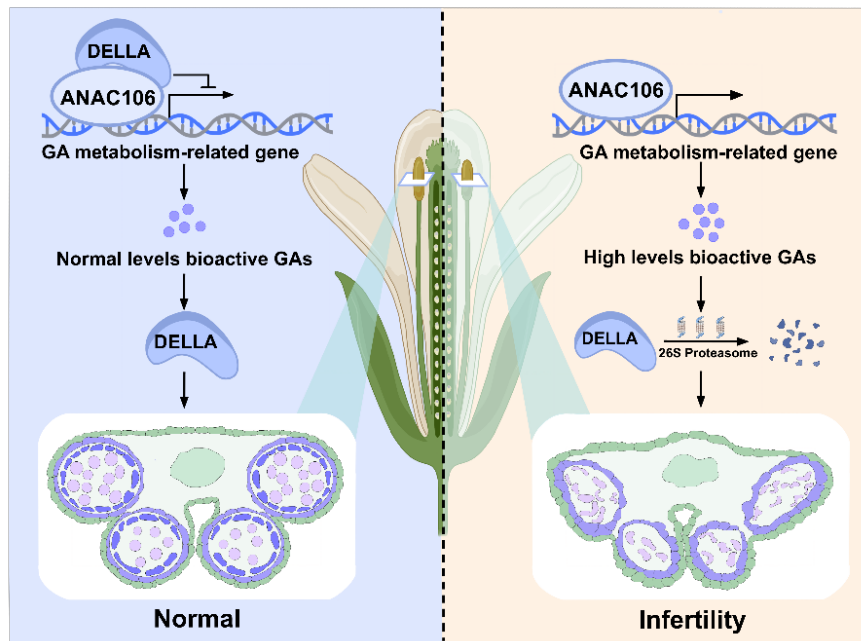


图 2、DELLA-ANAC106 分子模块调控 GA 合成及信号的稳态影响花粉发育的工作模型。

Figure 2. A working model illustrating the function of DELLA-ANAC106 feedback circuit in regulating pollen development by modulating the GA biosynthesis and signaling homeostasis.

3、MPK3/MPK6 信号决定胚乳细胞化时间从而调控种子大小

种子由受精后的胚珠发育而来，涉及一系列复杂的过程，包括来自母体的珠被(发育为种皮)、合子胚和胚乳三者的发育及相互之间的密切协同。三者共同决定了种子的大小。种子大小是作物最重要的产量性状之一。在模式植物拟南芥和其他重要作物中(如水稻)，种子大小关键调控途径是保守的，因此对种子大小调控机制的基础研究不仅对理解种子发育过程有着极为重要的科学意义，而且对作物高产具有非常重要的应用价值。

在前期研究中，我们及多个课题组发现 MKK4/MKK5-MPK3/MPK6 级联信号在拟南芥和水稻中均对种子大小发挥重要调控作用。近期有报道表明 MKK4/MKK5-MPK3/MPK6 级联位于类受体蛋白激酶 ER 下游，通过调控下游 DA1-UBP15 蛋白泛素酶体途径，调控珠被的发育从而影响种子大小。该报道部分阐明了 MPK3/MPK6 调控种子大小的机制，但是种子大小的决定涉及多个发育过程，详细全面的分子机制仍有待进一步阐明。我们的研究表明 MKK4/MKK5-MPK3/MPK6 级联通过调控胚乳细胞化的时间参与调控种子的大小。胚乳细胞化时间与种子大小密切相关：细胞化时间提前通常会导致种子变小，而细胞化延迟则会导致种子变大。MKK4/MKK5 或 MPK3/MPK6 缺失后都会导致其种子变小，并且胚乳细胞化的时间提前。在这个过程中，我们发现 WRKY 转录因子 MINI3/WRKY10 是 MPK3/MPK6 级联下游一个新的底物，参与调控种子的大小。WRKY10 蛋白在角果发育的早期表达，并且可以被 MPK3/MPK6 短暂的磷酸化，WRKY10 蛋白的磷酸化和胚乳细胞化的时间是密切相关的。模拟磷酸化失活形式的 WRKY10(WRKY10^{SA})突变蛋白的表达会干扰



WRKY10 正常的生物学功能, 不能恢复 *wrky10* 突变体种子变小的表型。而野生型 WRKY10 以及模拟磷酸化形式的 WRKY10^{SD} 均可以完全恢复 *wrky10* 突变体种子变小的表型。此外, 我们还通过组织表达分析、进化同源分析以及候选基因突变体表型分析, 发现了两个类受体蛋白激酶(Receptor-Like Kinase, RLK)IKU2 和 RLK7, 它们位于 MKK4/MKK5-MPK3/MPK6-WRKY10 上游参与调控种子的大小, 其中 RLK7 首次被发现参与调控种子的大小。此外, 我们通过 dual-LUC 实验发现, WRKY10 蛋白被 MPK3/MPK6 磷酸化后可以增强其对下游靶基因(*IKU2*, *RLK7* 和 *WRKY10*) 的转录激活能力, 从而形成一条正反馈信号通路。综上所述, 我们的研究发现了一条相对完整的信号通路, 即 IKU2/RLK7-MAPKKK(s)-MKK4/MKK5-MPK3/MPK6-WRKY10, 通过调控胚乳细胞化的时间而影响种子大小。鉴于 MAPK 在不同植物中功能的高度保守性, 因此该研究为作物高产提供了一个重要的理论依据。目前相关研究结果已投稿至 *Plant Cell* (under review)。

The MKK4/MKK5-MPK3/MPK6 Cascade Targets WRKY10 to Regulate Seed Endosperm Cellularization Downstream of IKU2 and RLK7

Seed size is a critical factor in determining crop yield. Recent studies highlighted the importance of MPK3/MPK6 cascade in regulating seed size in both *Arabidopsis* and rice. However, the underlying mechanism is not fully elucidated. Here, we report a novel function for the MKK4/MKK5-MPK3/MPK6 module in controlling the timing of endosperm cellularization, thereby regulating the seed size. Loss of function of MKK4/MKK5 or MPK3/MPK6 results in precocious endosperm cellularization and smaller seeds. WRKY transcription factor WRKY10/MINI3 is identified as a substrate of MPK3/MPK6 in this process. WRKY10 is expressed and phosphorylated by MPK3/MPK6 during the early stages of silique development, and it is degraded just before the initiation of endosperm cellularization. The phospho-deficient WRKY10^{SA} variant loses the function of wild-type WRKY10 *in vivo*. Furthermore, we found that IKU2 and RLK7, two closely related receptor-like kinases, function upstream of MKK4/MKK5-MPK3/MPK6-WRKY10 pathway to regulate seed size. The phosphorylation of WRKY10 mediated by MPK3/MPK6 enhances its transcriptional activity towards target genes, including *IKU2*, *RLK7*, and *WRKY10* itself, thereby forming a positive regulatory loop within this signaling pathway. Our study elucidates a signaling pathway composed of IKU2/RLK7-MAPKKK(s)-MKK4/MKK5-MPK3/MPK6-WRKY10 that regulates endosperm cellularization and seed size, providing a theoretical basis for crop breeding.

(二) 研究成果

发表论文: (*Corresponding author)

1. Zhang Y, Ge S, Dong L, Liu N, Shao S, Fan Z, Yang L, Si Q, Ye Y, Ren D, Zhang S, Xu J* (2024) Chemical-sensitized MITOGEN-ACTIVATED PROTEIN KINASE 4 provides insights into its functions in plant growth and immunity. *Plant Physiol* DOI: 10.1093/plphys/kiad574.



2. Zeng J, Duan M, Wang Y, Li G, You Y, Shi J, Liu C, Zhang J, Xu J, Zhang S, Zhao J* (2024) Sporophytic control of tapetal development and pollen fertility by a mitogen-activated protein kinase cascade in rice. *J Integrat Plant Biol* 66(7):1500-1516.

(三) 研究队伍

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附录、重要科研论文首页



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Maize smart-canopy architecture enhances yield at high densities

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Increasing planting density is a key strategy for enhancing maize yields^{1–3}. An ideotype for dense planting requires a ‘smart canopy’ with leaf angles at different canopy layers differentially optimized to maximize light interception and photosynthesis^{4–6}, among other features. Here we identified *leaf angle architecture of smart canopy 1* (*lac1*), a natural mutant with upright upper leaves, less erect middle leaves and relatively flat lower leaves. *lac1* has improved photosynthetic capacity and attenuated responses to shade under dense planting. *lac1* encodes a brassinosteroid C-22 hydroxylase that predominantly regulates upper leaf angle. Phytochrome A photoreceptors accumulate in shade and interact with the transcription factor RAVL1 to promote its degradation via the 26S proteasome, thereby inhibiting activation of *lac1* by RAVL1 and decreasing brassinosteroid levels. This ultimately decreases upper leaf angle in dense fields. Large-scale field trials demonstrate that *lac1* boosts maize yields under high planting densities. To quickly introduce *lac1* into breeding germplasm, we transformed a haploid inducer and recovered homozygous *lac1* edits from 20 diverse inbred lines. The tested doubled haploids uniformly acquired smart-canopy-like plant architecture. We provide an important target and an accelerated strategy for developing high-density-tolerant cultivars, with *lac1* serving as a genetic chassis for further engineering of a smart canopy in maize.

Global climate change, reductions in arable land and the growing world population pose grand challenges for food security and sustainable agriculture. To meet the increasing demands for food, global agricultural production needs to be doubled by 2050^{7,8}. Maize (*Zea mays*) is the most produced crop in the world, and serves as a major source of human food, livestock feed and industrial materials. Over the past few decades, continuous increases in planting densities have had a key role in yield gains in the USA—from around 30,000 plants per hectare in the 1930s to more than 80,000 plants per hectare currently^{1–3}. Similar trends were also observed in other countries, including China⁹. This success is largely attributed to the development of high-density-tolerant maize cultivars.

Optimal plant architecture is a prerequisite for adapting maize to dense planting. Leaf angle is a major trait that determines plant architecture. Upright leaf angles reduce mutual shading and increase solar irradiation penetration, thus improving photosynthetic efficiency at the population level to ultimately enhance grain yield under

dense planting^{3,4,10}. More upright leaves are selected in contemporary maize breeding^{3,11}. Within dense canopies typical of the maize field, leaves at different canopy layers receive distinct qualities and quantities of sunlight, which requires differential leaf orientation to maximize light interception and photosynthesis. Therefore, plant architecture ideal for dense planting does not simply require uniform upright leaf angles across the entire canopy, but instead needs an optimized distribution of leaf angles at different canopy layers. Ort et al.⁵ proposed an ideotype called a smart canopy, which includes optimized plant architecture together with improved biochemical features in leaves such as differential Rubisco catalytic capacities and photosystems across the plant⁵. In terms of architecture, a smart canopy features upright leaves in the upper canopy, less erect leaves in the middle canopy and relatively flat leaves in the lower canopy^{4–6}. Such canopy architecture would enable light to spread more evenly within a dense canopy, minimizing light saturation of the upper leaves and light starvation of the lower leaves^{4–6}.

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Substrate-induced condensation activates plant TIR domain proteins

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Plant nucleotide-binding leucine-rich repeat (NLR) immune receptors with an N-terminal Toll/interleukin-1 receptor (TIR) domain mediate recognition of strain-specific pathogen effectors, typically via their C-terminal ligand-sensing domains¹. Effector binding enables TIR-encoded enzymatic activities that are required for TIR–NLR (TNL)-mediated immunity^{2,3}. Many truncated TNL proteins lack effector-sensing domains but retain similar enzymatic and immune activities^{4,5}. The mechanism underlying the activation of these TIR domain proteins remain unclear. Here we show that binding of the TIR substrates NAD⁺ and ATP induces phase separation of TIR domain proteins in vitro. A similar condensation occurs with a TIR domain protein expressed via its native promoter in response to pathogen inoculation in planta. The formation of TIR condensates is mediated by conserved self-association interfaces and a predicted intrinsically disordered loop region of TIRs. Mutations that disrupt TIR condensates impair the cell death activity of TIR domain proteins. Our data reveal phase separation as a mechanism for the activation of TIR domain proteins and provide insight into substrate-induced autonomous activation of TIR signalling to confer plant immunity.

The perception of non-self molecules by the innate immune system of plants is mediated largely by two types of immune receptors¹. One type is cell membrane-localized pattern recognition receptors (PRRs). PRRs perceive features of microorganisms that are often conserved among widely related taxa in the extracellular space to elicit basal immunity, also referred to as pattern-triggered immunity⁶ (PTI). The second type is intracellular NLR receptors, which detect microorganism effectors inside plant cells to confer effector-triggered and pathogen strain-specific immunity⁷ (ETI). Activation of ETI results in termination of pathogen growth and often a localized, hypersensitive host cell death response at sites of attempted pathogen invasion⁷. Mounting evidence in *Arabidopsis thaliana* supports a crosstalk between PTI and ETI, which potentiates the immune response^{8–11}. Pathogen-detecting NLRs are divided into two main classes according to their N-terminal domains: coiled-coil NLRs (CNLRs) and TNLs¹². Upon recognition of pathogen effectors, CNLRs form resistosomes (pathogen-activated NLR oligomers) that can function as Ca²⁺-permeable channels^{13,14}. By contrast, effector binding to the C-terminal domains of TNLs induces the formation of tetrameric TNL resistosomes, enabling their TIR-encoded NADase activity^{2–5}. TNL resistosomes have an additional ADP-ribosylation activity¹⁵. The NADase and ribosyl-transferase activities of TIRs catalyse the production of small molecules which bind to and allosterically activate

dimers of the lipase-like protein ENHANCED DISEASE SUSCEPTIBILITY 1 (EDS1) and its direct partners PHYTOALEXIN DEFICIENT 4 (PAD4) or SENESCENCE-ASSOCIATED GENE 101 (SAG101)^{15,16}. Once activated, EDS1–PAD4 and EDS1–SAG101 dimers interact directly with downstream CNL-type helper NLRs, ACTIVATED DISEASE RESISTANCE 1 (ADRI) and N REQUIREMENT GENE 1 (NRG1), respectively, which presumably activates their Ca²⁺-permeable channel activity to mediate disease resistance and cell death^{15–18} (Extended Data Fig. 1a).

In addition to canonical TNLs, plant genomes encode many truncated TNLs that lack the C-terminal effector-sensing domains^{19,20}. In particular, monocotyledonous plants have TIR-only proteins but not TNLs²¹. Transient gene expression of such TIR domain proteins in *Nicotiana benthamiana* can be sufficient to trigger NADase-dependent cell death^{4,20,22,23}, suggesting that TNLs and TIRs share conserved signalling pathways. For example, the TIR-only protein RBA1 in *A. thaliana* accession Ag-0 responds to the bacterial pathogen effector HopBA1 to trigger EDS1-dependent ETI²³. Self-association mediated by conserved interfaces is important for the NADase and immune activities of TIRs^{23,24}. As well as ETI, TIR signalling also has a role in PTI and abiotic stress responses^{10,11,25}. PTI elicitors induce activation of TIR signalling, which in turn boosts the PTI response^{10,11}, whereas pathogen effector binding is required to stimulate the enzymatic activities of TNLs^{2,3}. TIR domain

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The ZmWAKL–ZmWIK–ZmBLK1–ZmRBOH4 module provides quantitative resistance to gray leaf spot in maize

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Gray leaf spot (GLS), caused by the fungal pathogens *Cercospora zea-maydis* and *Cercospora zeina*, is a major foliar disease of maize worldwide (*Zea mays* L.). Here we demonstrate that *ZmWAKL* encoding cell-wall-associated receptor kinase-like protein is the causative gene at the major quantitative disease resistance locus against GLS. The *ZmWAKL*^Y protein, encoded by the resistance allele, can self-associate and interact with a leucine-rich repeat immune-related kinase *ZmWIK* on the plasma membrane. The *ZmWAKL*^Y/*ZmWIK* receptor complex interacts with and phosphorylates the receptor-like cytoplasmic kinase (RLCK) *ZmBLK1*, which in turn phosphorylates its downstream NADPH oxidase *ZmRBOH4*. Upon pathogen infection, *ZmWAKL*^Y phosphorylation activity is transiently increased, initiating immune signaling from *ZmWAKL*^Y, *ZmWIK*, *ZmBLK1* to *ZmRBOH4*, ultimately triggering a reactive oxygen species burst. Our study thus uncovers the role of the maize *ZmWAKL*–*ZmWIK*–*ZmBLK1*–*ZmRBOH4* receptor/signaling/executor module in perceiving the pathogen invasion, transducing immune signals, activating defense responses and conferring increased resistance to GLS.

Plants have evolved multiple, varied signal reception/transduction mechanisms to control cellular functions and coordinate defense responses at the cellular, tissue and organismal levels. The initial perception of pathogen infection is mediated by pattern-recognition receptors (PRRs) at the plasma membrane, which include receptor-like kinases (RLKs) and receptor-like proteins^{1,2}. The detection of pathogen-associated molecular patterns and damage-associated molecular patterns by cognate PRRs leads to pattern-triggered immunity (PTI), which includes rapid reactive oxygen species (ROS)

production, calcium (Ca²⁺) influx, activation of calcium-dependent and mitogen-activated kinases, changes of immune-related gene expression and, in some cases, localized cell death^{3–5}. PTI is vital for preventing infection of most nonadapted microbes and restricting the growth of adapted microbes, termed basal resistance⁶.

Cell-wall-associated kinases (WAKs) and WAK-like kinases (WAKLs) represent a unique class of RLKs that are major regulators of fungal disease resistance in plant species. In *Arabidopsis*, *WAKL22/RF01* confers resistance to a broad spectrum of *Fusarium* races⁷. The maize

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The ZmCPK39–ZmDi19–ZmPR10 immune module regulates quantitative resistance to multiple foliar diseases in maize

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Gray leaf spot, northern leaf blight and southern leaf blight are three of the most destructive foliar diseases affecting maize (*Zea mays* L.). Here we identified a gene, *ZmCPK39*, that encodes a calcium-dependent protein kinase and negatively regulates quantitative resistance to these three diseases. The *ZmCPK39* allele in the resistant line displayed significantly lower pathogen-induced gene expression than that in the susceptible line. A marked decrease in *ZmCPK39* abundance mitigated the phosphorylation and degradation of the transcription factor ZmDi19. This led to elevated expression of *ZmPR10*, a gene known to encode an antimicrobial protein, thereby enhancing maize resistance to foliar diseases. Moreover, the F₁ hybrid with reduced *ZmCPK39* expression favored disease resistance, thereby increasing yield. Hence, the discovery of the ZmCPK39–ZmDi19–ZmPR10 immune module provides insight into the mechanisms underlying broad-spectrum quantitative disease resistance and also offers a new avenue for the genetic control of maize foliar diseases.

Gray leaf spot (GLS), northern leaf blight (NLB) and southern leaf blight (SLB) caused by the necrotrophic fungal pathogens *Cercospora zae-maydis* and *Cercospora zeina*¹, *Exserohilum turcicum*² and *Cochliobolus heterostrophus*³, respectively, are among the most destructive foliar diseases in maize (*Zea mays* L.). Documented yield losses of maize due to GLS ranged from 10% to 60% (refs. 4–6). GLS and NLB were the foliar diseases causing the greatest estimated yield losses in the United States and Ontario, Canada, from 2012 to 2019 (refs. 7,8). SLB caused a hugely damaging epidemic in the United States in 1970 and is still a consistently damaging disease worldwide^{9–11}.

Resistance to NLB is controlled by both race-specific major effect (qualitative) genes and by nonrace-specific quantitative trait loci (QTL)

with minor effects^{12,13}. All known maize resistance to GLS and SLB is controlled by QTL, most with small or moderate additive effects^{14,15}. The existence of QTL controlling broad-spectrum resistance to GLS, NLB and SLB has long been indicated, as significant correlations between resistances to all three foliar diseases were observed¹⁶. Some genes have been identified, mediating resistance to GLS (*ZmWAKO2* and *ZmWAKL*)^{17,18}, NLB (*Ht1*, *Ht2/Ht3* and *Htn1*)^{19–21}, SLB (*ZmAPX1*, *ChSK1* and *ZmAGO18b*)^{22–24} and to multiple foliar diseases (*ZmCCoAOMT2*, *ZmMMI1* and *ZmNANMT*)^{25–27}.

The calcium ion (Ca²⁺) is a ubiquitous intracellular second messenger and has long been recognized as an essential mediator in plant immunity. In plants, Ca²⁺-dependent protein kinases (CPKs) harbor

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ARTICLE OPEN



The LRR receptor-like kinase ALR1 is a plant aluminum ion sensor

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Plant survival requires an ability to adapt to differing concentrations of nutrient and toxic soil ions, yet ion sensors and associated signaling pathways are mostly unknown. Aluminum (Al) ions are highly phytotoxic, and cause severe crop yield loss and forest decline on acidic soils which represent ~30% of land areas worldwide. Here we found an *Arabidopsis* mutant hypersensitive to Al. The gene encoding a leucine-rich-repeat receptor-like kinase, was named Al Resistance1 (ALR1). Al ions binding to ALR1 cytoplasmic domain recruits BAK1 co-receptor kinase and promotes ALR1-dependent phosphorylation of the NADPH oxidase RbohD, thereby enhancing reactive oxygen species (ROS) generation. ROS in turn oxidatively modify the RAE1 F-box protein to inhibit RAE1-dependent proteolysis of the central regulator STOP1, thus activating organic acid anion secretion to detoxify Al. These findings establish ALR1 as an Al ion receptor that confers resistance through an integrated Al-triggered signaling pathway, providing novel insights into ion-sensing mechanisms in living organisms, and enabling future molecular breeding of acid-soil-tolerant crops and trees, with huge potential for enhancing both global food security and forest restoration.

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INTRODUCTION

Aluminum (Al) is the most abundant metal in the Earth's crust (~8% by weight). However, the Al ion is highly toxic to plants. When soils become acidic, part of Al is solubilized from insoluble aluminosilicates or oxides to form soluble ions.¹ The resultant phytotoxic Al ions can rapidly enter root cells, and cause a series of cellular damages,² thus inhibiting root growth and function of most plants at very low micromolar concentrations.³ These effects substantially reduce crop yields, particularly when combined with other stresses, such as drought and nutrient deficiency. Al toxicity is therefore recognized as the major factor limiting agricultural productivity on acid soils which occupy ~30% of territorial land area and up to 50% of the potential arable lands worldwide, and is exceeded only by drought among abiotic limitations to crop production.^{4,5} Moreover, Al toxicity is an important contributor to forest decline,⁶ posing a real threat to the global ecological environment.

Decades of research have established the central role of the secretion of organic acid anions (including malate, citrate and oxalate) in Al resistance in the main crops.^{3,7,8} These anions chelate and restrict Al ions from entering the root apex, the primary site of Al toxicity.² Genetically enhancing their biosynthesis or extrusion significantly increases crop Al resistance and growth on acid soils.^{9,10} In *Arabidopsis*, *Al-ACTIVATED MALATE*

TRANSPORTER 1 (*AtALMT1*, the major contributor of Al resistance in *Arabidopsis*) and *MULTI-DRUG and TOXIC COMPOUND EXTRUSION* (*MATE*) respectively encode malate and citrate efflux channels/transporters conferring its resistance to Al toxicity.^{11,12} The Al-induced expression of both genes is exclusively controlled by the zinc finger transcription factor SENSITIVE TO PROTON TOXICITY 1 (*STOP1*), the central regulator of Al resistance.^{12,13} *STOP1* has widespread conservation of function in Al resistance in different plant species.^{14,15} Whilst *STOP1* mRNA abundance is largely unresponsive to Al,¹³ Al promotes *STOP1* protein accumulation in root cell nuclei, and its accumulation is regulated by the F-box protein REGULATION OF *ATALMT1* EXPRESSION 1 (*RAE1*), which targets *STOP1* degradation via the ubiquitin-26S proteasome pathway.¹⁶ Additionally, *STOP1* is also regulated by SUMOylation and phosphorylation.^{17,18} Nevertheless, how Al ions are perceived and then connected to the accumulation of the *STOP1* central regulator remains unknown.

Plant receptor-like kinases (RLKs), function as cell surface receptors for steroid hormone, chemical or peptide signals.^{19–23} We hence wondered whether RLKs might similarly serve in Al perception and/or signaling. A typical RLK consists of a ligand-binding extracellular domain, a single transmembrane domain, and a cytoplasmic serine/threonine kinase domain.²⁴ The *Arabidopsis*

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New mechanistic insights into phosphate-starvation-regulated plant architecture change and nutrient uptake

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Phosphorus (P) is an indispensable macro-nutrient for plant growth that is absorbed by plants in the form of inorganic phosphate (Pi). Pi deficiency is a major challenge limiting crop productivity worldwide. To combat Pi scarcity and maintain Pi homeostasis, plants have evolved different strategies for efficient Pi acquisition (Paz-Ares et al., 2022). Plants reduce overall growth and enhance the root system to optimize nutrients foraging in Pi-limited soils. Strigolactones (SLs), renowned for their roles as rhizosphere signals and phytohormones in plant development, play a significant role in integrating nitrate and Pi signals to regulate shoot and root development. Nevertheless, the molecular mechanisms underlying the integration of SL signaling in Pi starvation regulated shoot or root architecture, and the balance between P and nitrogen (N) uptake remain largely unexplored.

Recently, Yuan et al. (2023) found that NSP1 and NSP2, which are induced at the transcription level by PHR2 under low-Pi conditions, form a complex to directly bind the promoter of SL biosynthesis genes, thereby markedly enhancing SL biosynthesis in rice. In this spotlight, we highlight and discuss the research progress regarding the molecular mechanisms by which SL mediates shoot and root development and N-P interaction under Pi-starvation conditions (Figure 1).

THE PHR2-NSP1/2 MODULE MEDIATES SHOOT AND ROOT GROWTH RESPONSE TO LOW PI

In their recent study, Yuan et al. (2023) investigated the molecular mechanism underlying rice tiller development regulated by NSP1 and NSP2 under Pi deficiency. The *nsp1*, *nsp2*, and *nsp1 nsp2* mutants showed relatively more tiller numbers compared to wild type (WT) under Pi-sufficient soils. Furthermore, the inhibitory effects of low Pi on tiller number were less pronounced in *nsp1*, *nsp2*, and *nsp1 nsp2* (Yuan et al., 2023). This suggests that NSP1 and NSP2 are involved in regulating tiller number in response to Pi deficiency. Consistently, the tiller number response to low Pi in the SL receptor mutant *d14* was significantly reduced. In addition, previous results indicated that the effect of Pi deficiency on tiller bud outgrowth was considerably weakened in SL biosynthesis mutant *d10* and SL signaling mutant *d3* (Umehara et al., 2010). These results suggest that SL signaling is involved in tiller repression under Pi deficiency. In the absence of Pi, with the increase of SL biosynthesis, the SL signaling suppressor DWARF53 (D53) proteins are rapidly degraded, thereby promoting the expression of *TEOSINTE*

BRANCHED 1 to reduce rice tiller numbers (Jiang et al., 2013; Zhou et al., 2013). Similarly, D53 protein levels decreased much more slowly in *nsp1 nsp2* mutants than in WT under Pi-deficient conditions. Compared to Pi-sufficient conditions, the SL levels (e.g., 4-deoxyorobanchol) in WT root were greatly increased (up to 600-fold) under Pi deficiency; however, the SL levels were not obviously induced in roots of *nsp1*, *nsp2*, or *nsp1 nsp2* mutants under Pi-deficient conditions (Yuan et al., 2023). These findings indicate that NSP1 and NSP2 play important roles in tiller number repression under Pi deficiency by promoting SL synthesis. SL synthesis or signaling mutants still show tiller repression under Pi deficiency, suggesting that other signaling pathways participate in the regulation of tiller development under low-Pi conditions. Yuan et al. (2023) revealed that NSP1 and NSP2 form heteromeric complexes and bind directly to the promoters of SL synthesis genes *D27*, *D17*, *D10*, *Os900*, and *Os1400* to regulate the transcript levels of these genes under Pi deficiency. Consistently, it has been reported in *Medicago truncatula* that MtNSP1 and MtNSP2 are required for SL accumulation by regulating the expression of *D27* in response to Pi deficiency (Liu et al., 2011), suggesting that the functions of NSP transcription factors in SL synthesis are conserved among different plant species.

Furthermore, the authors demonstrated that *NSP1* and *NSP2* act as direct downstream genes of *OsPHR2*, which can also activate the expression of *D27* and *Os900* as previous studies have shown (Das et al., 2022; Song et al., 2022). These results indicate that NSP1/2 and *OsPHR2* work synergistically to regulate the SL biosynthesis under Pi-limited conditions. Although both *OsPHR2* and NSP1–NSP2 directly regulate the transcription of SL-biosynthesis-related genes, the presence of the NSP1–NSP2 module may amplify Pi-deficient signaling and enhance the expression of SL biosynthesis genes.

SL affects lateral root (LR) formation and root hair density under low-Pi conditions. Sun et al. (2014) reported that low Pi increases primary root length and decreases LR density in an SL-dependent manner by downregulating most of the PIN-family auxin transporter genes (Sun et al., 2014). Yuan et al. (2023) indicated that auxin transporter genes were enriched in the downregulated genes under active SL treatment, demonstrating an interaction between SL and auxin in root system architecture formation. The

Genetic variation in a heat shock transcription factor modulates cold tolerance in maize

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ABSTRACT

Understanding how maize (*Zea mays*) responds to cold stress is crucial for facilitating breeding programs of cold-tolerant varieties. Despite extensive utilization of the genome-wide association study (GWAS) approach for exploring favorable natural alleles associated with maize cold tolerance, few studies have successfully identified candidate genes that contribute to maize cold tolerance. In this study, we used a diverse panel of inbred maize lines collected from different germplasm sources to perform a GWAS on variations in the relative injured area of maize true leaves during cold stress—a trait very closely correlated with maize cold tolerance. We identified *HSF21*, which encodes a B-class heat shock transcription factor (HSF) that positively regulates cold tolerance at both the seedling and germination stages. Natural variations in the promoter of the cold-tolerant *HSF21*^{Hap1} allele led to increased *HSF21* expression under cold stress by inhibiting binding of the basic leucine zipper bZIP68 transcription factor, a negative regulator of cold tolerance. By integrating transcriptome deep sequencing, DNA affinity purification sequencing, and targeted lipidomic analysis, we revealed the function of *HSF21* in regulating lipid metabolism homeostasis to modulate cold tolerance in maize. In addition, we found that *HSF21* confers maize cold tolerance without incurring yield penalties. Collectively, this study establishes *HSF21* as a key regulator that enhances cold tolerance in maize, providing valuable genetic resources for breeding of cold-tolerant maize varieties.

Key words: heat shock factor HSF21, cold tolerance, natural variation, bZIP68, lipid metabolism, maize

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INTRODUCTION

Maize (*Zea mays*) is inherently vulnerable to low temperatures owing to its tropical origin (Matsuoka et al., 2002). Low temperatures have a significant impact on the growth and development of maize, affecting its planting range, sowing period, and growth duration (Allen and Ort, 2001). There is therefore an urgent demand for maize varieties with robust cold tolerance. Over the past two decades, considerable efforts have been devoted to identifying genes that influence cold-related traits through quantitative trait locus analysis and genome-wide association study (GWAS)

(Jompuk et al., 2005; Presterl et al., 2007; Leipner et al., 2008; Strigens et al., 2013; Yi et al., 2021; Zhang et al., 2021). However, many proposed candidate genes or their causal variants have not yet been clearly validated and clarified.

Lipid remodeling is one strategy employed by plants to endure cold stress (Miquel et al., 1993; Okuley et al., 1994; Moellering

Proximate profiling reveals a conserved SGT1-NSL1 signaling module that activates NLR-mediated immunity

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ABSTRACT

Suppressor of G2 allele of *skp1* (SGT1) is a highly conserved eukaryotic protein that plays a vital role in growth, development, and immunity in both animals and plants. Although some SGT1 interactors have been identified, the molecular regulatory network of SGT1 remains unclear. SGT1 serves as a co-chaperone to stabilize protein complexes such as the nucleotide-binding leucine-rich repeat (NLR) class of immune receptors, thereby positively regulating plant immunity. SGT1 has also been found to be associated with the SKP1-Cullin-F-box (SCF) E3 ubiquitin ligase complex. However, whether SGT1 targets immune repressors to coordinate plant immune activation remains elusive. In this study, we constructed a toolbox for TurboID- and split-TurboID-based proximity labeling (PL) assays in *Nicotiana benthamiana* and used the PL toolbox to explore the SGT1 interactome during pre- and post-immune activation. The comprehensive SGT1 interactome network we identified highlights a dynamic shift from proteins associated with plant development to those linked with plant immune responses. We found that SGT1 interacts with Necrotic Spotted Lesion 1 (NSL1), which negatively regulates salicylic acid-mediated defense by interfering with the nucleocytoplasmic trafficking of non-expressor of pathogenesis-related genes 1 (NPR1) during N NLR-mediated response to tobacco mosaic virus. SGT1 promotes the SCF-dependent degradation of NSL1 to facilitate immune activation, while salicylate-induced protein kinase-mediated phosphorylation of SGT1 further potentiates this process. Besides N NLR, NSL1 also functions in several other NLR-mediated immunity. Collectively, our study unveils the regulatory landscape of SGT1 and reveals a novel SGT1-NSL1 signaling module that orchestrates plant innate immunity.

Key words: suppressor of G2 allele of *skp1*, SGT1, proximity labeling, N NLR immune receptor, Necrotic Spotted Lesion 1, NSL1, salicylic acid, ubiquitination

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INTRODUCTION

Plants often confront various environmental stresses because of their sessile lifestyle. To cope with pathogen attacks, plants have evolved cell surface-localized pattern recognition receptors (PRRs) that enable them to detect pathogen invasions and initiate pathogen-associated molecular patterns (PAMPs) and trigger PAMP-triggered immunity (PTI), which provides basal

resistance to pathogens. However, to establish an infection, pathogens secrete effectors to perturb PTI, leading to effector-triggered susceptibility (ETS). Plants have evolved with the intracellular nucleotide-binding leucine-rich repeat (NLR) class of

A maize WAK-SnRK1 α 2-WRKY module regulates nutrient availability to defend against head smut disease

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ABSTRACT

Obligate biotrophs depend on living hosts for nutrient acquisition to complete their life cycle, yet the mechanisms by which hosts restrict nutrient availability to pathogens remain largely unknown. The fungal pathogen *Sporisorium reilianum* infects maize seedlings and causes head smut disease in inflorescences at maturity, while a cell wall-associated kinase, ZmWAK, provides quantitative resistance against it. In this study, we demonstrate that *S. reilianum* can rapidly activate ZmWAK kinase activity, which is sustained by the 407th threonine residue in the juxtamembrane domain, enabling it to interact with and phosphorylate ZmSnRK1 α 2, a conserved sucrose non-fermenting-related kinase α subunit. The activated ZmSnRK1 α 2 translocates from the cytoplasm to the nucleus, where it phosphorylates and destabilizes the transcription factor ZmWRKY53. The reduced ZmWRKY53 abundance leads to the downregulation of genes involved in transmembrane transport and carbohydrate metabolism, resulting in nutrient starvation for *S. reilianum* in the apoplast. Collectively, our study uncovers a WAK-SnRK1 α 2-WRKY53 signaling module in maize that conveys phosphorylation cascades from the plasma membrane to the nucleus to confer plant resistance against head smut in maize, offering new insights and potential targets for crop disease management.

Key words: head smut disease, *Sporisorium reilianum*, ZmWAK, SnRK1 α 2, phosphorylation, nutrient

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INTRODUCTION

Biotrophic pathogens compete with their host plants for nutrients during long-term endophytic growth (Kretschmer et al., 2022; Zhu et al., 2023). While pathogens secrete apoplastic effectors to induce nutrient susceptibility, little is known regarding how the hosts establish immunity strategies to counteract pathogen invasions. The rich-nutrient extracellular apoplast of the host is a competitive battlefield where microbial pathogens race to uptake required metabolites (Toruno et al., 2016). Bacterial pathogens target the transporters via type III secretion systems to promote sugar efflux for bacterial nutrition (Chen et al., 2010). Pattern recognition receptors (PRRs) also activate sugar transporters to enhance monosaccharide uptake, reducing sugar availability for bacterial growth (Yamada et al., 2016). However, it is still poorly understood whether host plants proactively regulate apoplastic metabolites levels upon infection to combat pathogenic fungi.

Maize head smut, caused by the biotrophic fungal pathogen *Sporisorium reilianum*, is a soil-borne disease that results in significant losses in maize production worldwide. This pathogen invades maize seedlings by penetrating the roots or coleoptile, and then grows through the mesocotyl to reach the above-ground tissues. Once *S. reilianum* enters male or female inflorescences, it shifts from a vegetative to a reproductive growth mode, forming massive fungal sori. These fungal spores, capable of surviving in the soil for years, germinate under favorable conditions and initiate a new infection cycle in maize during the subsequent growing season (Sabbagh et al., 2009).

Located on the plasma membrane, PRRs detect pathogen-associated signatures, triggering immune responses against

Liquid–liquid phase separation of TZP promotes PPK-mediated phosphorylation of the phytochrome A photoreceptor

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Phytochrome A (phyA) is the plant far-red (FR) light photoreceptor and plays an essential role in regulating photomorphogenic development in FR-rich conditions, such as canopy shade. It has long been observed that phyA is a phosphoprotein *in vivo*; however, the protein kinases that could phosphorylate phyA remain largely unknown. Here we show that a small protein kinase family, consisting of four members named PHOTOREGULATORY PROTEIN KINASES (PPKs) (also known as MUT9-LIKE KINASES), directly phosphorylate phyA *in vitro* and *in vivo*. In addition, TANDEM ZINC-FINGER/PLUS3 (TZP), a recently characterized phyA-interacting protein required for *in vivo* phosphorylation of phyA, is also directly phosphorylated by PPKs. We reveal that TZP contains two intrinsically disordered regions in its amino-terminal domain that undergo liquid–liquid phase separation (LLPS) upon light exposure. The LLPS of TZP promotes colocalization and interaction between PPKs and phyA, thus facilitating PPK-mediated phosphorylation of phyA in FR light. Our study identifies PPKs as a class of protein kinases mediating the phosphorylation of phyA and demonstrates that the LLPS of TZP contributes significantly to more production of the phosphorylated phyA form in FR light.

Phytochromes are the plant photoreceptors that perceive the environmental red (R) (600–700 nm) and far-red (FR) (700–750 nm) light signals to modulate plant growth and development throughout the plant life cycle^{1–3}. Recent studies have indicated that phytochromes also function as thermosensors at ambient temperatures^{4–7}. Phytochromes

exist in two interconvertible forms: the Pr form and the Pfr form, which have absorption peaks in R and FR light, respectively^{1,2,8}. The Pfr form of phytochromes has long been believed to be the biologically active form; however, the nuclear-localized Pr form was recently suggested to have biological activity⁹. In darkness, phytochromes are synthesized in the Pr

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A clade of receptor-like cytoplasmic kinases and 14-3-3 proteins coordinate inositol hexaphosphate accumulation

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Inositol hexaphosphate (InsP₆) is the major storage form of phosphorus in seeds. Reducing seed InsP₆ content is a breeding objective in agriculture, as InsP₆ negatively impacts animal nutrition and the environment. Nevertheless, how InsP₆ accumulation is regulated remains largely unknown. Here, we identify a clade of receptor-like cytoplasmic kinases (RLCKs), named Inositol Polyphosphate-related Cytoplasmic Kinases 1-6 (IPCK1-IPCK6), deeply involved in InsP₆ accumulation. The InsP₆ concentration is dramatically reduced in seeds of *ipck* quadruple (*T-4m/C-4m*) and quintuple (*C-5m*) mutants, accompanied with the obviously increase of phosphate (Pi) concentration. The plasma membrane-localized IPCKs recruit IPK1 involved in InsP₆ synthesis, and facilitate its binding and activity via phosphorylation of GRF 14-3-3 proteins. IPCKs also recruit IPK2s and PI-PLCs required for InsP₄/InsP₅ and InsP₃ biosynthesis respectively, to form a potential IPCK-GRF-PLC-IPK2-IPK1 complex. Our findings therefore uncover a regulatory mechanism of InsP₆ accumulation governed by IPCKs, shedding light on the mechanisms of InsP biosynthesis in eukaryotes.

Inositol hexaphosphate (InsP₆), also known as phytic acid, is ubiquitous in eukaryotes and regulates a plenty of cellular functions, including stress responses¹, development² and phosphate (Pi) homeostasis³. As the overall high amount of P in plant seeds (e.g. cereal and legume seeds), InsP₆ nevertheless cannot be efficiently digested by humans and nonruminants⁴. The undigested InsP₆ not only reduces the bioavailability of essential mineral elements (e.g. Fe, Zn, and Ca) and amino acids in the digestive tract, but also is considered a leading source of phosphorus pollution from agriculture when excreted in animal waste^{5,6}. Therefore, reducing InsP₆ content in seeds is one of the important breeding objectives in agriculture. Although efforts have

been made in some species, such as maize and rice^{2,3}, the very limited understanding on the regulatory mechanisms of InsP₆ biosynthetic pathway has hampered this breeding activity.

In the mature seeds, InsP₆ is stored and organized in globoids⁷. During the seed germination stage, InsP₆ is hydrolyzed to release Pi and mineral elements, which provide nutrients and energy for the early growth of seedlings^{4,6}. InsP₆ also plays an important role in the triggering of Ca²⁺ signals, the auxin storage and transport, phosphatidylinositol signaling, cell wall synthesis and the production of secondary metabolites^{1,3,4,8}. InsP₆ can be formed by two different pathways: a lipid-dependent pathway, where phospholipase C (PI-PLC) catalyzes

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ZmGDI α -hel counters the RBSDV-induced reduction of active gibberellins to alleviate maize rough dwarf virus disease

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Maize rough dwarf disease (MRDD) threatens maize production globally. The P7-1 effector of the rice black-streaked dwarf virus (RBSDV) targets maize Rab GDP dissociation inhibitor alpha (ZmGDI α) to cause MRDD. However, P7-1 has difficulty recruiting a ZmGDI α variant with an alternative *helitron*-derived exon 10 (ZmGDI α -hel), resulting in recessive resistance. Here, we demonstrate that P7-1 can recruit another maize protein, gibberellin 2-oxidase 13 (ZmGA2ox7.3), which also exhibits tighter binding affinity for ZmGDI α than ZmGDI α -hel. The oligomerization of ZmGA2ox7.3 is vital for its function in converting bioactive gibberellins into inactive forms. Moreover, the enzymatic activity of ZmGA2ox7.3 oligomers increases when forming hetero-oligomers with P7-1/ZmGDI α , but decreases when ZmGDI α -hel replaces ZmGDI α . Viral infection significantly promotes ZmGA2ox7.3 expression and oligomerization in ZmGDI α -containing susceptible maize, resulting in reduced bioactive GA₁/GA₄ levels. This causes an auxin/cytokinin imbalance and ultimately manifests as MRDD syndrome. Conversely, in resistant maize, ZmGDI α -hel counters these virus-induced changes, thereby mitigating MRDD severity.

Plant viruses, primarily transmitted by biotic vectors, pose a significant threat to global food security by inflicting substantial damage to crops¹. To combat viral infections, plants have evolved multiple layers of defense responses, which are collectively referred to as active resistance². In addition, plants have developed passive resistance strategies, enabling them to evade viral recognition or exploitation by modifying or eliminating susceptibility factors, also referred to as recessive resistance³. Most of the naturally-occurring recessive resistance genes are related to the translation initiation factors eIF4E and eIF4G or their homologs⁴. Other loss-of-susceptibility genes include ZmGDI α -hel, cPGK2, HvPDIL5-1, and among others^{5–7}.

Maize rough dwarf disease (MRDD) is a devastating viral disease, often referred to as the “cancer” of maize. It was first reported in the late 1940s in northern Italy and subsequently spread to countries such

as Greece, France, and Israel⁸. MRDD is caused by various *Fijivirus* pathogens in the family *Reoviridae*, among which the maize rough dwarf virus was detected in Europe, Mal de Rio Cuarto virus was reported in South America, and the major pathogen responsible in East Asia is the rice black-streaked dwarf virus (RBSDV)^{9,10}. RBSDV is transmitted to maize in a persistent manner by the small brown planthopper (*Laodelphax striatellus*)¹¹. The typical symptoms of MRDD are characterized by severe growth abnormalities, including dwarfism, shortened internodes, abnormal ears/tassels, dark-green leaves, and white waxy enations on the backs of leaf veins¹². RBSDV has a genome of 10 double-stranded RNAs (S1–S10), with sizes ranging from 1.8 to 4.5 kb^{13,14}. Each segment encodes one or, in the case of S5, S7, and S9, two proteins¹³. Notably, the P7-1 effector, encoded by S7-1, forms tubular structures in RBSDV-infected plants and localizes to

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Endomembrane trafficking driven by microtubule growth regulates stomatal movement in *Arabidopsis*

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Microtubule-based vesicle trafficking usually relies upon kinesin and dynein motors and few reports describe microtubule polymerisation driving directional vesicle trafficking. Here we show that *Arabidopsis* END BINDING1b (EB1b), a microtubule plus-end binding protein, directly interacts with SYP121, a SNARE protein that mediates the trafficking of the K⁺ channel KAT1 and its distribution to the plasma membrane (PM) in *Arabidopsis* guard cells. Knockout of AtEB1b and its homologous proteins results in a modest but significant change in the distribution of KAT1 and SYP121 in guard cells and consequently delays light-induced stomatal opening. Live-cell imaging reveals that a portion of SYP121-associated endomembrane compartments co-localise with AtEB1b at the growing ends of microtubules, trafficking along with the growth of microtubules for targeting to the PM. Our study reveals a mechanism of vesicle trafficking driven by microtubule growth, which is involved in the redistribution of PM proteins to modulate guard cell movement.

Spatial positioning and motility of endomembrane compartments and organelles are fundamental to cellular functions in all eukaryotic cells and are primarily governed by the cytoskeleton. Microtubule-based vesicle trafficking and organelle positioning are commonplace in animal cells and are known to depend on kinesin and dynein motor proteins^{1–3}. In plant cells, it has long been accepted that directional vesicle motility is predominantly dependent on actin-based myosin motors^{4,5}. Later on, however, researchers reveal a critical role for microtubules in endoplasmic reticulum (ER) motility and morphology⁶, in insertion and tethering of cellulose synthase complexes to the plasma membrane (PM)^{7,8} and in endocytic recycling of the auxin efflux carrier PIN2 to the PM in plants⁹. It has been proposed that microtubules and their motors might anchor or slow down organelles/vesicles for their targeting to appropriate destinations. In addition, the plus-end binding protein, CLASP (CLIP-170 ASSOCIATED PROTEIN), was shown to mediate the association of sorting endosomes with microtubules¹⁰. Interestingly, intracellular small cellulose synthases-containing compartments were reported to tether with

microtubules, and track with the depolymerising ends of microtubules⁸, which suggests a role for microtubule dynamics in organelle motility. Yet reports of microtubule growth-based directional vesicle trafficking in plant cells are lacking.

Stomata are surrounded by a pair of guard cells and are present on the epidermis of all aerial parts of almost all angiosperm. In response to various hormonal and environmental stimuli, such as abscisic acid, light and atmospheric CO₂ levels, as well as abiotic and biotic stresses, guard cells precisely regulate photosynthetic gas exchange and water transpiration, and restrict pathogen invasion by regulating stomatal opening and closing^{11–17}. During stomatal movement, the volume of each guard cell changes rapidly, driven by the transport of K⁺, Cl[−] and other solutes across the PM and guard cell tonoplast, with consequent effects on the osmotic content of the cell and its turgor^{15,18}. In this process, vesicle trafficking of ion channels in guard cells contributes to stomatal movement^{19,20}. It has been demonstrated that the regulation of the recycling of the K⁺ channel KAT1 to the PM is important for stomatal movement. Furthermore, delivery and positional anchoring

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Article

Diurnal regulation of alternative splicing associated with thermotolerance in rice by two glycine-rich RNA-binding proteins

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ABSTRACT

Rice (*Oryza sativa* L.) production is threatened by global warming associated with extreme high temperatures, and rice heat sensitivity is differed when stress occurs between daytime and nighttime. However, the underlying molecular mechanism are largely unknown. We show here that two glycine-rich RNA binding proteins, OsGRP3 and OsGRP162, are required for thermotolerance in rice, especially at nighttime. The rhythmic expression of *OsGRP3/OsGRP162* peaks at midnight, and at these coincident times, is increased by heat stress. This is largely dependent on the evening complex component OsELF3-2. We next found that the double mutant of *OsGRP3/OsGRP162* is strikingly more sensitive to heat stress in terms of survival rate and seed setting rate when comparing to the wild-type plants. Interestingly, the defect in thermotolerance is more evident when heat stress occurred in nighttime than that in daytime. Upon heat stress, the double mutant of *OsGRP3/OsGRP162* displays globally reduced expression of heat-stress responsive genes, and increases of mRNA alternative splicing dominated by exon-skipping. This study thus reveals the important role of *OsGRP3/OsGRP162* in thermotolerance in rice, and unravels the mechanism on how *OsGRP3/OsGRP162* regulate thermotolerance in a diurnal manner.

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1. Introduction

Rice (*Oryza sativa* L.) is the staple food for more than half of the world's population. An increasing human population demands more rice productivity, which is challenged by a more adverse climate associated with extreme weather conditions [1]. Based on mathematical modeling, world-wide cereal production is estimated to have a loss of 6%–7% yield per 1 °C increase in seasonal mean temperature associated with extreme heat disasters [2]. In the past century, daily minimum temperature in nighttime increased more than daily maximum temperature in daytime [3]. Crops, such as rice, have different sensitivity to heat stress between day and night and among different varieties [4–6]. However, how this diurnal difference in thermotolerance is acquired in plants remains elusive.

The circadian clock is a ubiquitous controlling system that allows plants to coordinate their growth and development with day and night signals. It maintains a roughly 24-h rhythm of internal biological process [7]. This circadian oscillation is generated by a number of repressors and activators that are integrated into multiple interconnected feedback loops [8,9]. Many circadian clock

regulators are involved in plant responses to warm temperatures [10]. For example, early flowering 3 (ELF3), one of the evening complex (EC) components that are night-time repressors in the circadian circuit, inhibits hypocotyl growth in *Arabidopsis* at ambient temperature, and it is subjected to liquid-liquid separation and proteasome-mediated protein degradation under warm temperature conditions [10–12]. In contrast, the expression of *ELF4*, another important component of EC, is also tightly regulated by reveille 5 (RVE5), RVE7, circadian clock associated 1 (CCA1) and late elongation hypocotyl (LHY), either positively or negatively under warm temperature conditions in *Arabidopsis* [13]. Interestingly, RVE4 and RVE8 regulate the first wave of heat stress responses in the day, but confers thermotolerance in the evening in *Arabidopsis* [14]. These results suggest that plant growth and survival under high temperature conditions are dependent on the time of day when high temperature occurs, however, factors that provide temporal resistance in a diurnal manner await discovery.

In the current study, we show that *OsGRP3/OsGRP162* convey diurnal signals downstream of EC, and regulate diurnal thermotolerance in rice. Furthermore, we show that *OsGRP3/OsGRP162* bind to various mRNAs and interact with spliceosomal components to regulate alternative splicing. Collectively, these results demonstrate that *OsGRP3/OsGRP162* are required for rice plants to maintain high yielding in response to nighttime heat stress.

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News & Views

3D chromatin reorganization during stress responses in plants

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Being sessile, plants evolve different acclimation strategies at both the transcriptional and post-translational levels to cope with adverse environmental conditions [1]. Several recent studies [2–9] have shown that gene expression at transcriptional level under abiotic stress conditions is associated with highly dynamic three-dimensional (3D) chromatin reorganization, opening up a new research direction on the role of epigenetic modification and nucleoskeleton maintenance in impacting 3D chromatin architecture and stress-responsive gene expression in plants.

Chromatin is mainly composed of basic structural units called nucleosomes, in which naked DNA is wrapped with histone octamers (two copies of H3, H4, H2A, H2B) in eukaryotes [10]. Chromatin is further packaged into 3D structures including loops, topologically associating domains (TADs), compartments, and territory. Chromatin interactions play a crucial role in gene regulation by bringing distal regulatory elements, such as enhancers and promoters, into close proximity, facilitating the formation of transcriptional complexes and the regulation of gene expression in response to unfavorable environments in plants. As demonstrated by high-throughput chromosome conformation capture (Hi-C) and 3D-fluorescence *in situ* hybridization (3D-FISH), the chromatin accumulated in the specific area of nucleus is called chromatin territory; and the internal region of chromatin preferentially interacts to form TAD structures; TADs are modified by active and repressive histone marks, which constitute A compartments with high transcriptional rate and B compartments with low transcriptional rate, respectively, in plants [11]. TAD structures play a major role in chromatin packing of wide genome in animals, however, the model of TAD structures is under debate in plants. Due to the low number of defined TAD structures in plants relative to that in animals [12], TADs may not represent the whole chromatin state in plants. Further, in animals, cohesin complexes extrude chromatin via their ring-like shape until the chromatin joins at specific CCCTC-binding factor (CTCF) binding sites by two convergent CTCF zinc finger proteins, which forms TADs to shape loop conformation and induce gene expression [13]. In plants such as maize (*Zea mays*) and tomato (*Solanum lycopersicum*), chromatin loops are often formed in local A compartments between gene islands segmented by local B compartments [11]. Plants have conserved cohesin proteins but lack the CTCF homologues compared with animals [2]. Deletion of the core cohesin gene *RCE8* shows meiotic defects in chromatin

compaction, while deletion of either switch defective/sucrose non-fermentable (SWI/SNF), imitation switch (ISWI), inositol requiring 80 (INO80), or chromodomain helicase DNA-binding (CHD) chromatin remodeling complex protein affects nucleosome distribution pattern as well as nucleosome density in *Arabidopsis thaliana* [2]. Further observations in rice (*Oryza sativa*) suggest that thousands of distinct TAD boundaries are associated with euchromatic epigenetic marks and active gene expression, and enriched with a consensus sequence recognized by plant-specific TCP proteins [12]. Therefore, plant TADs may have different structural features compared to those in animals.

Chromatin loop recruits distal locus together to elicit co-expression networks. In mammals, two classes of “gained” and “stable” enhancer-promoter contacts are observed in terminal differentiation through genome-wide promoter capture Hi-C (Chi-C) [14]. Later research also reveals that long-range interactions between distal *cis*-regulatory elements (CREs) and promoters play major roles in maize [15]. For example, it is common that silencer-like regulatory elements with clusters of H3K27me3 form long-range chromatin interactions with distal genes to silence gene transcription [3]. Recent studies show that long-range H3K27me3-marked chromatin loops are dependent on Polycomb group (PcG) proteins associated with the coregulation of specific gene clusters in *Arabidopsis*, which is also conserved in rice and soybean (*Glycine max*) [4]. However, how the chromatin loop regulates gene transcription awaits further investigation.

The overall structure of chromatin architecture is dynamic depending on different cell types, different developmental stages, and different environmental conditions (Fig. 1). The relationship between chromatin reorganization and transcriptional reprogramming under stress conditions is very attractive and has received much attention in recent years. For example, heat stress disrupts the silence state of heterochromatin-associated transposable elements (TEs) due to the rearrangement of chromatin interaction regions. Further analysis in *Arabidopsis* reveals that activation of TEs is highly associated with chromatin decondensation between pericentromeres and distal intra-chromosomal regions [5]. Furthermore, heat activation of TEs exhibits a high correlation with the reduction of chromosomal interactions [12]. In contrast, cold stress increases A-B compartment interaction, reducing the spatial constraints on chromosomal compartments and decreasing long-range interactions on the same chromosome over 1 Mb distance in rice [12]. By comparing the chromatin structure changes (i.e., A/B compartments transition, TAD size, long-range interactions)

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Differential phosphorylation of Ca²⁺-permeable channel CYCLIC NUCLEOTIDE-GATED CHANNEL20 modulates calcium-mediated freezing tolerance in Arabidopsis

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Abstract

Plants respond to cold stress at multiple levels, including increasing cytosolic calcium (Ca²⁺) influx and triggering the expression of cold-responsive genes. In this study, we show that the Ca²⁺-permeable channel CYCLIC NUCLEOTIDE-GATED CHANNEL20 (CNGC20) positively regulates freezing tolerance in Arabidopsis (*Arabidopsis thaliana*) by mediating cold-induced Ca²⁺ influx. Moreover, we demonstrate that the leucine-rich repeat receptor-like kinase PLANT PEPTIDE CONTAINING SULFATED TYROSINE1 RECEPTOR (PSY1R) is activated by cold, phosphorylating and enhancing the activity of CNGC20. The *psy1r* mutant exhibits decreased cold-evoked Ca²⁺ influx and freezing tolerance. Conversely, COLD-RESPONSIVE PROTEIN KINASE1 (CRPK1), a protein kinase that negatively regulates cold signaling, phosphorylates and facilitates the degradation of CNGC20 under prolonged periods of cold treatment, thereby attenuating freezing tolerance. This study thus identifies PSY1R and CRPK1 kinases that regulate CNGC20 activity and stability, respectively, thereby antagonistically modulating freezing tolerance in plants.

IN A NUTSHELL

Background: Cold stress is a major environmental factor that adversely affects plant growth and development. Plants have developed a series of complex mechanisms at multiple levels to acclimate to cold stress, including increasing cytosolic calcium (Ca²⁺) influx and triggering the expression of cold-responsive genes. Several Ca²⁺-permeable channels, such as plasma membrane-localized CYCLIC NUCLEOTIDE -GATED CHANNELSs (CNGCs), have been shown to play critical roles in cold-induced Ca²⁺ signaling in plants. However, how CNGC is fine-tuned in response to cold stress remains unclear.

Question: How do plants finely tune calcium signaling in response to cold stress?

Findings: In this study, we revealed that CNGC20 plays an important role in regulating plant freezing tolerance and cold-induced Ca²⁺ influx in Arabidopsis (*Arabidopsis thaliana*). At the early stages of cold response, the receptor-like kinase, PLANT PEPTIDE CONTAINING SULFATED TYROSINE 1 RECEPTOR (PSY1R), is rapidly activated and phosphorylates CNGC20, which enhances its channel activity, leading to the increase in cold-induced Ca²⁺ influx, thus positively regulates CBFs expression and freezing tolerance. In addition, Cold-responsive protein kinase 1 (CRPK1), a negative regulator of plant freezing tolerance, phosphorylates CNGC20 to facilitate its degradation during the prolonged cold stress, thereby attenuating freezing tolerance of plants. This study reveals that PSY1R and CRPK1 target distinct sites of CNGC20 for phosphorylation to regulate CNGC20 activity and stability, respectively, thereby fine-tuning plant freezing tolerance.

Next steps: How PSY1R and CRPK1 are activated in response to cold stress is an important question. Moreover, the dynamics of CNGC-mediated cold-induced calcium signature await further investigation.

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The plant rhabdovirus viroporin P9 facilitates insect-mediated virus transmission in barley

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Abstract

Potassium (K⁺) plays crucial roles in both plant development and immunity. However, the function of K⁺ in plant–virus interactions remains largely unknown. Here, we utilized *Barley yellow striate mosaic virus* (BYSMV), an insect-transmitted plant cytorhabdovirus, to investigate the interplay between viral infection and plant K⁺ homeostasis. The BYSMV accessory P9 protein exhibits viroporin activity by enhancing membrane permeability in *Escherichia coli*. Additionally, P9 increases K⁺ uptake in yeast (*Saccharomyces cerevisiae*) cells, which is disrupted by a point mutation of glycine 14 to threonine (P9^{G14T}). Furthermore, BYSMV P9 forms oligomers and targets to both the viral envelope and the plant membrane. Based on the recombinant BYSMV–GFP (BYGFP) virus, a P9-deleted mutant (BYGFP^{ΔP9}) was rescued and demonstrated infectivity within individual plant cells of *Nicotiana benthamiana* and insect vectors. However, BYGFP^{ΔP9} failed to infect barley plants after transmission by insect vectors. Furthermore, infection of barley plants was severely impaired for BYGFP–P9^{G14T} lacking P9 K⁺ channel activity. In vitro assays demonstrate that K⁺ facilitates virion disassembly and the release of genome RNA for viral mRNA transcription. Altogether, our results show that the K⁺ channel activity of viroporins is conserved in plant cytorhabdoviruses and plays crucial roles in insect-mediated virus transmission.

Introduction

Potassium (K⁺) is an essential and abundant macronutrient in plant cells and plays fundamental roles in enzyme activation, membrane transport, osmoregulation, and cellular homeostasis (Wang and Wu 2017). Since available K⁺ concentration in soils is very low, plants can sense low K⁺ (LK) stress and enhance K⁺ uptake from environment (Wang et al. 2021). Intracellular K⁺ homeostasis is important for plant adaptive responses to abiotic and biotic stresses (Wang et al. 2021). Thus, application of K⁺ fertilizer improves crop health and decreases incidence of fungal and bacterial diseases in most cases (Amtmann et al. 2008; Wang et al. 2013; Wang and Wu 2017). Nonetheless, it remains elusive whether the K⁺ status plays positive or negative roles in controlling viral diseases (Amtmann et al. 2008). Moreover, whether and how plant viruses modulate plant K⁺ homeostasis and immunity are also largely unknown.

Most animal viruses encode small hydrophobic viroporins that can enhance membrane permeability through ion channel activity. Viroporins are commonly composed of 60 to 120 amino acids with a highly hydrophobic transmembrane domain (TMD). Viroporins usually form hydrophilic pores within host cell membranes for influx of ions and small molecules (Gonzalez and Carrasco 2003; Nieva et al. 2012; Scott and Griffin 2015). Viroporins participate in virus entry, replication, assembly, release, and disruption of host physiological processes (Gonzalez and Carrasco 2003; Nieva et al. 2012; Scott and Griffin 2015). The influenza A virus (IAV) M2 protein was first reported to exhibit viroporin activity (Pinto et al. 1992), which has been used as an

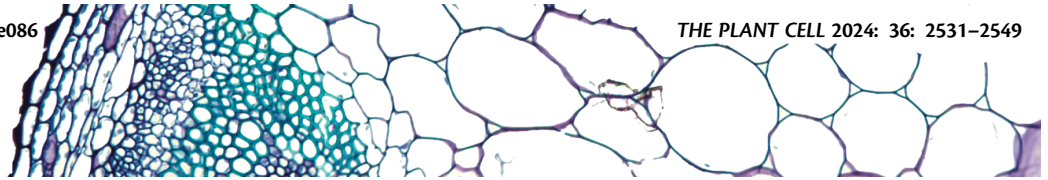
antiviral target for chemical compounds (Scott and Griffin 2015). In addition, viroporin-defective virus mutants have been generated as attenuated vaccines (Watanabe et al. 2009). Therefore, characterization of viroporins has received substantial attention over the past decades. However, analogous functions of viroporins in plant viruses and their interplay with plant ion homeostasis remain to be uncovered.

The Rhabdoviridae is a family of negative-stranded RNA viruses with a wide range of hosts including plants, vertebrates, and invertebrates (Walker et al. 2022). All rhabdoviruses share similar genome organization, encoding 5 conserved structural proteins, 3′–N (nucleocapsid protein)–P (phosphoprotein)–M (matrix protein)–G (glycoprotein)–L (large polymerase)–5′ in a negative polarity. The G–L gene junction commonly contains an accessory gene encoding a putative viroporin in animal rhabdoviruses (Walker et al. 2011; Walker et al. 2022). The α1 protein of Bovine ephemeral fever virus (BEFV), a typical rhabdovirus of the genus *Ephemerovirus*, has been identified as a viroporin (Joubert et al. 2014), but its functions in viral infection remain unexplored.

Plant rhabdoviruses severely affect crop productivity worldwide by infecting economically important monocot and dicot plants (Bejerman et al. 2021). Plant rhabdoviruses usually encode 4 to 5 accessory proteins interspersed between the gene junctions of N–P, P–M, and G–L (Walker et al. 2011). However, functions of these genes are predicted but not experimentally validated in the context of virus infections due to lack of virus reverse genetics systems (Zang et al. 2020; Li and Zhao 2021). Despite technical challenges, the past decade has witnessed progress in reverse genetics systems of plant rhabdoviruses. *Sonchus yellow net*

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The adaptor protein ECAP, the corepressor LEUNIG, and the transcription factor BEH3 interact and regulate microsporocyte generation in Arabidopsis

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Abstract

Histospecification and morphogenesis of anthers during development in Arabidopsis (*Arabidopsis thaliana*) are well understood. However, the regulatory mechanism of microsporocyte generation at the pre-meiotic stage remains unclear, especially how archesporial cells are specified and differentiate into 2 cell lineages with distinct developmental fates. *SPOROCTELESS* (*SPL*) is a key reproductive gene that is activated during early anther development and remains active. In this study, we demonstrated that the EAR motif-containing adaptor protein (ECAP) interacts with the Gro/Tup1 family corepressor LEUNIG (*LUG*) and the BES1/BZR1 HOMOLOG3 (*BEH3*) transcription factor to form a transcription activator complex, epigenetically regulating *SPL* transcription. *SPL* participates in microsporocyte generation by modulating the specification of archesporial cells and the archesporial cell-derived differentiation of somatic and reproductive cell layers. This study illustrates the regulation of *SPL* expression by the ECAP–LUG–BEH3 complex, which is essential for the generation of microsporocytes. Moreover, our findings identified ECAP as a key transcription regulator that can combine with different partners to regulate gene expression in distinct ways, thereby facilitating diverse processes in various aspects of plant development.

Introduction

The stamen is the male reproductive organ in flowering plants that contains a 4-lobed anther on top of a filament. Anther development is a complex process that can be divided into 14 stages based on histological features. Stage 1 is marked by the emergence of the rounded stamen primordia with 3 layers (L1, L2, and L3), and the anther dehiscing to liberate mature pollen grains denotes the final stage (Stage 14; Sanders et al. 1999; Scott et al. 2004; Alvarez-Buylla

et al. 2010). Stages 1 to 5 denote the pre-meiotic period of anther development, during which the cells of the L2 layer undergo a complex series of divisions and give rise to most of the cell types of the anther to form the 4 radially symmetrical locules/microsporangia (1 for each lobe). Archesporial cells are the founder cells of the microsporangia, which arise in the 4 corners of the L2 layer during Stage 2. Next, periclinal division of archesporial cells generates the primary parietal layer (which then divides and differentiates into the endothecium, middle layer, and tapetum) and the primary

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EXECUTER1 and singlet oxygen signaling: A reassessment of nuclear activity

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Abstract

Chloroplasts are recognized as environmental sensors, capable of translating environmental fluctuations into diverse signals to communicate with the nucleus. Among the reactive oxygen species produced in chloroplasts, singlet oxygen ($^1\text{O}_2$) has been extensively studied due to its dual roles, encompassing both damage and signaling activities, and the availability of conditional mutants overproducing $^1\text{O}_2$ in chloroplasts. In particular, investigating the Arabidopsis (*Arabidopsis thaliana*) mutant known as *fluorescent (flu)* has led to the discovery of EXECUTER1 (EX1), a plastid $^1\text{O}_2$ sensor residing in the grana margin of the thylakoid membrane. $^1\text{O}_2$ -triggered EX1 degradation is critical for the induction of $^1\text{O}_2$ -responsive nuclear genes (SORNGs). However, a recent study showed that EX1 relocates from chloroplasts to the nucleus upon $^1\text{O}_2$ release, where it interacts with WRKY18 and WRKY40 (WRKY18/40) transcription factors to regulate SORNG expression. In this study, we challenge this assertion. Our confocal microscopy analysis and subcellular fractionation assays demonstrate that EX1 does not accumulate in the nucleus. While EX1 appears in nuclear fractions, subsequent thermolysin treatment assays indicate that it adheres to the outer nuclear region rather than localizing inside the nucleus. Furthermore, luciferase complementation imaging and yeast 2-hybrid assays reveal that EX1 does not interact with nuclear WRKY18/40. Consequently, our study refines the current model of $^1\text{O}_2$ signaling by ruling out the nuclear relocation of intact EX1 as a means of communication between the chloroplast and nucleus.

Introduction

Singlet oxygen ($^1\text{O}_2$) is a nonradical reactive oxygen species (ROS) produced either through photosensitizers such as free tetrapyrrole molecules including chlorophyll and its precursors or via lipid peroxidation-derived lipid radicals, i.e. light-dependent or light-independent $^1\text{O}_2$, respectively (op den Camp et al. 2003; Apel and Hirt 2004; Wagner et al. 2004; Kim et al. 2012; Dogra et al. 2018, 2022; Tano et al. 2023). Light-dependent $^1\text{O}_2$ is generated within chloroplasts and exhibits a dual role. On the one hand, it poses a potential threat due to its high reactivity with macromolecules, and on the other, it serves as a signaling molecule that contributes to various biological processes, including growth inhibition and cell death.

The investigation of 2 Arabidopsis (*Arabidopsis thaliana*) mutants, *chlorina 1 (chl1)* and *fluorescent (flu)*, has proven instrumental in unraveling the complexities of $^1\text{O}_2$ -signaling pathways (Meskauskiene et al. 2001; Ramel et al. 2013a, 2013b). In *chl1*, the absence of CHLOROPHYLLIDE A OXYGENASE (CAO) intensifies photoinhibition in Photosystem II (PSII) due to the lack of chlorophyll *b* synthesis, leading to the light-intensity-dependent overproduction of $^1\text{O}_2$. This heightened sensitivity to light-induced damage is a hallmark of the *chl1* mutant. Conversely, the *flu* mutant exhibits a unique behavior, conditionally generating $^1\text{O}_2$ within chloroplasts when transitioning from darkness to light. This intriguing phenomenon is attributed to the FLU protein's role as a negative feedback regulator of protochlorophyllide

(Pchl) in dark conditions (Kauss et al. 2012; Wang et al. 2022). Consequently, the loss of FLU results in the excessive accumulation of free Pchl, a potent photosensitizer, within chloroplasts. Upon exposure to light, free Pchl efficiently transfers the absorbed light energy to ground-state oxygen molecules, thereby generating $^1\text{O}_2$.

Through extensive investigation of these $^1\text{O}_2$ -overproducing mutants, researchers have identified 2 putative $^1\text{O}_2$ sensors: β -carotene and the EXECUTER1 (EX1) protein. These sensors are localized in distinct regions of thylakoid membranes. β -Carotene operates in the grana core (appressed areas of grana), where active and inactive PSII complexes generate $^1\text{O}_2$ (Dogra et al. 2018). Excessive light is shown to trigger the oxidation of β -carotene, leading to the production of volatile retrograde signaling molecules, including β -cyclocitral (β -CC). β -CC, in turn, induces the expression of nuclear genes encoding detoxification proteins, mitigating oxidative stress (D'Alessandro et al. 2020).

In contrast, the majority of EX1 proteins accumulate in the grana margin (nonappressed regions of grana), where they interact with certain chlorophyll synthesis enzymes, especially Pchl oxidoreductases and the machinery responsible for PSII repair, including filamentous temperature-sensitive H (FtsH) proteases (Wang et al. 2016; Dogra et al. 2019b, 2022). Notably, FtsH2 protease promotes EX1 degradation following $^1\text{O}_2$ release. FtsH2-dependent EX1 turnover is integral to initiating $^1\text{O}_2$ signaling, as genetic inactivation of FtsH2 disrupts EX1-mediated $^1\text{O}_2$

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