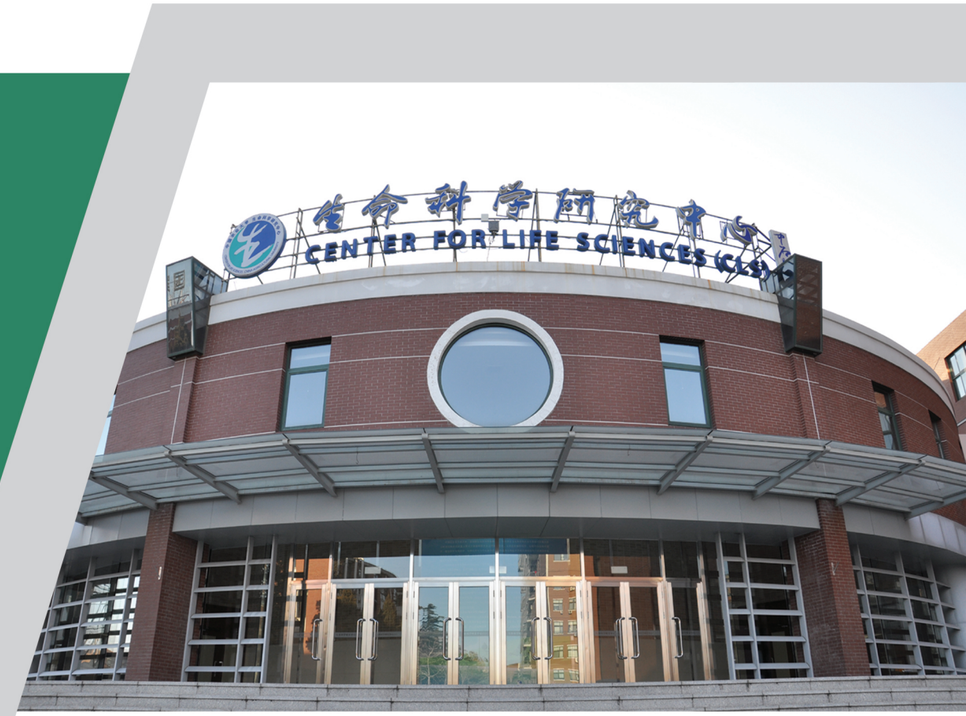
SKLPPB

地址：北京市海淀区圆明园西路 2 号
中国农业大学　生命科学研究中心
邮编：100193
电话：010-62733475
传真：010-62733491
电子邮箱：ppbskl@chinalab.gov.cn
网址：http://sklppb.cau.edu.cn/

2022年报

植物生理学与生物化学国家重点实验室

2022 年报 ANNUAL REPORT



植物生理学与生物化学国家重点实验室

State Key Laboratory of Plant Physiology and Biochemistry

2022 年报

目 录

一、实验室概况

植物生理学与生物化学国家重点实验室是在原农业部中国农业大学植物生理生化开放实验室的基础上建立的。2001 年 11 月通过专家论证，2002 年 1 月经科技部正式批准建设，2003 年 10 月 16 日通过建设验收，正式进入国家重点实验室行列，2006 年、2011 年和 2017 年通过国家重点实验室评估，其中在 2011 年的国家重点实验室的评估中被评为优秀类实验室。

实验室总体定位：实验室以创新性基础研究为主，兼顾相关的应用基础研究。实验室的总体研究方向是“植物抗逆和水分、养分高效利用的生理生化及分子生物学基础”。实验室的主要研究工作内容是“系统深入地探讨植物响应高盐、低温、水分和养分亏缺等非生物逆境胁迫的信号转导、基因表达及生理生化调控机理”。

实验室主要研究方向：围绕“植物抗逆、高效的生理生化及分子生物学基础”的总体研究方向，实验室设立五个主要研究方向：（1）植物/作物抗逆的生理生化及分子生物学基础；（2）植物/作物水分、养分和光高效利用的分子生理学机制；（3）植物/作物复杂环境下的生长可塑性调控机理；（4）作物抗逆高效的分子设计和种质创新；（5）作物抗逆高效性状的化学调控技术及应用。

实验室主要研究内容：植物/作物细胞响应非生物逆境胁迫的跨膜信号转导机制；植物/作物细胞响应非生物逆境胁迫的细胞内信号转导机制；植物/作物响应非生物逆境胁迫的基因转录调控分子机制；作物（玉米）抗逆相关性状的重要新基因的克隆和功能分析；植物/作物应答逆境胁迫的信号转导、转录调控的整合生物学机制；农作物抗逆高效的化学调控机理及应用技术研究。

实验室总体建设发展目标：围绕植物科学领域及我国实现资源节约型、环境友好型农业可持续发展中的重大科学问题和国家需求开展基础及应用基础研究工作，在保持实验室整体研究水平在国内同类实验室处于领先水平的同时，力争尽快使本实验室成为国际同领域中具有重要影响力和竞争力的科学研究和人才培养基地。在基础研究方面，集中优势力量重点探索植物响应及适应干旱、高盐、低温、营养亏缺等逆境胁迫的信号转导网络调控机制及分子遗传机理等重要理论科学问题，发表有突出创新意义并在国际上有重要影响的研究论文。在应用基础研究方面，克隆一批有重要应用价值、有我国自主知识产权的重要农艺性状基因，并努力开展作物（玉米）功能基因组及种质创新和新品种培育研究；同时还将植物生长发育的激素调控理论应用于作物栽培生产实践，以建立重要农作物高产高效的化学调控栽培技术体系等。在人才培养方面，实验室将努力加强年轻科技人才的培养，达到平均每年培养 5～8 名博士后、25～30 名博士生、10～15 名访问学者或进修人员的能力，强化国家理科生物学基地本科生的科研训练工作。在实验室运行管理方面，切实实施“开放、联合、流动、竞争”的运行机制，与其他院校及研究单位充分共享实验材料、仪器设备、数据和技术等各类公共资源，使人员与学术的交流常态化，实现我国植物生理生化及植物分子生物学和生物技术领域研究力量间的强强联合与优势互补，将本实验室建设成为我国植物科学领域优秀研究人才的聚集和培养基地及创新性高水平研究成果的重要产出基地。

在国内外相关学科领域中的地位和影响，及在国家科技发展中的作用：植物抗逆高效的生理及分子生物学基础研究不仅是植物科学基础研究的前沿领域，而且与农作物生产及农业可持续发展的重大需求密切相关。

研究各种外界环境因子对植物生长发育的影响一直是植物科学研究领域的重要命题，探索相关的重要科学问题既有重要的理论意义，也与农作

物育种和栽培实践密切相关。植物是如何感受各种环境刺激信号的？植物通过何种机制响应和适应各种环境胁迫？植物在逆境下生长发育的分子机制为何？植物在逆境下如何调控细胞的活性？植物响应环境胁迫的细胞信号转导及基因表达调控机理为何？植物适应环境胁迫的分子遗传调控网络机制为何？如何通过调控重要功能基因或调控因子的表达或活性来改良农作物的抗逆高效性状？诸如此类问题是当今植物科学研究领域的前沿和热点，亟待深入的探索。因此，解析植物感受和响应各种环境胁迫的生理及分子机制是植物科学基础理论研究不可或缺的重要方面。

农作物生产中的淡水、土地、肥料资源的严重匮乏及农业生态环境的恶化已严重制约我国农业的可持续发展。我国三分之二以上面积的耕地属干旱和半干旱耕地，近三分之一面积的耕地受到不同程度盐渍化的影响，而且盐渍化耕地面积还在逐年增加。我国还有10亿亩以上的荒地和滩涂是盐碱地。受全球气候变化和温室效应的影响，极端温度出现的频率日益增多，我国北方大部分地区和南方的早春、晚秋季节的农作物生产频繁遭受低温冷害，致使作物减产甚至绝收。我国磷、钾等矿产资源匮乏，每年耗巨资进口磷、钾化肥，农作物生产中磷钾肥施用量不足严重限制了作物产量的提高，而且还由于养分供应不平衡造成了氮肥浪费及由此带来的环境污染。综上所诉，干旱、盐碱、低温、磷钾亏缺等非生物逆境胁迫已成为制约我国农业可持续发展的重要因素。

要实现我国农业长远可持续发展的战略目标，必须走资源高效利用、环境友好型可持续发展之路，以期逐步实现农业生产方式的根本转变。已有的研究表明，同种作物的不同基因型或不同种类作物的耐干旱、盐碱、低温性状以及对土壤矿质养分的需求和吸收利用能力是不同的，表明植物的这些抗逆性状是受遗传控制的。因此，利用分子育种技术培育抗逆作物优良品种在理论上是可行的。而利用现代作物分子育种技术培育作物抗逆

新品种首先依赖于对植物适应环境胁迫的分子调控机理的认识。因此，开展对植物适应环境胁迫的分子调控机理及抗逆性状分子遗传机制的研究是我国农业可持续发展的重大和迫切需求。

本实验室围绕植物科学基础理论研究领域的重要科学问题，同时瞄准我国农作物生产可持续发展的重大需求，长期坚持“植物抗逆、高效的生理及分子生物学基础”方面的创新性研究，对我国植物科学学科发展及农作物抗逆高效研究方面有着重要的作用和意义。实验室目前已形成一支以优秀学术带头人为核心的高水平研究队伍，凝聚了一批具有发展潜力的中青年学术骨干，已成为吸引优秀年轻归国学者优先选择的实验室之一。目前实验室承担了一大批国家重大科研任务，不断取得一些重要研究成果，其中有些研究成果已在国内外学术界产生重要影响。

本实验室现有固定人员 73 人，其中中科院院士 1 人、教育部重大人才工程特聘教授 13 人、教育部重大人才工程青年学者 38 人、国家自然科学基金创新研究群体 4 个等。在 73 位固定人员中包括教授 46 人、副教授 18 人、中级研究人员和科研辅助人员 9 人，其中专职或兼职的实验技术平台管理人员 10 人。

2022 年度实验室执行各类研究项目 105 项，包括国家自然科学基金委创新研究群体 2 项，国家自然科学基金杰出青年基金 4 项、优秀青年基金 3 项、重点项目/重大 10 项，国际（地区）合作与交流项目 4 项，联合基金 3 项、面上项目 40 项。科技部国家重点研发/重大专项 10 项，横向项目 8 项，其他项目 21 项，经费合计 10647 万元。另外，2022 年获得重点实验室专项经费 913.75 万元，其中设置自主研究项目 23 项，经费合计 510 万元。

2022 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 70 篇，其中 *Science* 1 篇，*Mol Plant* 4 篇，*Nat Plants* 1 篇，*Nat Commun*

3 篇，*Sci Adv* 1 篇，*Dev Cell* 2 篇，*Plant Cell* 11 篇，*Curr Biol* 1 篇，*Trends Biotechnol* 1 篇，*Trends Biochem Sci* 1 篇，另有影响因子 9-12 的论文 12 篇，影响因子 7-9 的论文 21 篇等，累计 SCI 影响因子 805，平均影响因子 11.5/篇。实验室另外发表 28 篇合作研究论文。2022 年度实验室获得发明专利和软件著作权 34 项。

2022 年实验室学术交流活动 107 人次，其中邀请国内外同行来实验室讲学 42 人次，实验室人员在国内外参加会议并报告 19 人次，实验室人员在国内外讲学 46 人次。实验室组织“研究生系列报告”12 次，有 36 位博士研究生做了报告。

2022 年实验室培养研究生共 600 人（中国农业大学 492 人，浙江大学 108 人），在读直博生和博士生共 443 人，硕士生 157 人，其中博士毕业 63 人，硕士毕业 19 人。2022 年实验室有博士后 56 人。

植物生理学与生物化学国家重点实验室

State Key Laboratory of Plant Physiology and Biochemistry

http://sklppb.cau.edu.cn/

二、实验室组织机构

实验室 主　任：杨淑华　教　授

实验室 副主任：郭　岩　教　授

郑绍建　教　授

王　毅　教　授

刘采菲　副教授

学术委员会　主　任：种　康　院士（中国科学院植物研究所）

学术委员会　副主任：曹晓风　院士（中国科学院遗传与发育生物学研究所）

巩志忠　教授（中国农业大学）

学术委员会　委　员：

林鸿宣　院　士（中国科学院分子植物科学卓越创新中心）

朱健康　院　士（南方科技大学）

万建民　院　士（中国农业科学院作物科学研究所）

钱　前　院　士（中国农业科学院作物科学研究所）

薛勇彪　研究员（中国科学院北京基因组研究所）

瞿礼嘉　教　授（北京大学）

宋纯鹏　教　授（河南大学）

戚益军　教　授（清华大学）

李召虎　教　授（中国农业大学）

孙传清　教　授（中国农业大学）

李建生　教　授（中国农业大学）

郭　岩　教　授（中国农业大学）

杨淑华　教　授（中国农业大学）

郑绍建　教　授（浙江大学）

学术委员会秘书：王　毅　教　授（中国农业大学）

三、2022 年学术委员会会议纪要

时　间：2023 年 2 月 11 日（星期六）9:00-12:00

地　点：中国农业大学 生命科学研究中心 第七会议室（4057 室）

校外专家线上

四、2022 年重要成果简介

（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，解析了干旱胁迫负调控因子 RAF22 调控拟南芥抗旱的分子机制，发现蛋白激酶 RAF22 与磷酸酶 ABI1 和蛋白激酶 OST1 形成动态调控网络，在优化植物生长和环境适应方面发挥着关键作用（Sun et al., *Mol Plant*, 2022, 巩志忠课题组）。

在植物响应盐胁迫研究方面，解析了盐胁迫下玉米 Dirigent（DIR）家族蛋白 ZmSTL1/ZmESBL 调控凯氏带可塑性，维持 Na^+稳态，增强植物耐盐性的机制（Wang et al., *Nat Commun*, 2022, 蒋才富课题组）；阐明了磷酸酶 PP2C D6 和 D7 作为 SOS1 的负调控元件，调节植物耐盐性的分子机理（Fu et al., *Plant Cell*, 2022, 郭岩课题组）。

在植物低温胁迫应答方面，利用高分辨质谱对玉米关联群体进行低温处理下的非靶标代谢组学分析，结合 mGWAS 分析，解析了转录因子 ZmICE1 参与调控氨基酸代谢和玉米耐低温的分子机制（Jiang et al., *Nat Plants*, 2022, 杨淑华课题组）；阐释了转录因子 bZIP68 在玉米早期驯化中受自然选择调控玉米耐冷性的分子机理（Li et al., *Plant Cell*, 2022, 杨淑华课题组）；发现拟南芥钙依赖蛋白激酶 CPK28 和转录因子 NLP7 参与感知并解码低温诱导的特异 Ca^{2+}信号，介导低温信号快速从细胞膜传递至细胞核，调控低温特异的转录组重塑（Ding et al., *Sci Adv*, 2022, 杨淑华课题组）。为庆祝《*Developmental Cell*》建刊 20 周年，受邀撰写植物感知和应答温度胁迫的综述论文（Ding et al., *Dev Cell*, 2022, 杨淑华课题组）。

在植物高温胁迫应答方面，发现 ERdj3B 调控拟南芥胚珠的发育，并参与热胁迫响应过程，揭示了 SDF2-ERdj3B-BiP 分子伴侣复合体对 ERECTA 家族受体激酶质量控制的分子机理（Leng et al., *Plant Cell*, 2022, 陈立群课题组）；发现转录抑制因子 RVE5 在温和高温下与转录抑制因子 CCA1 竞争调节 *ELF4* 的表达从而调控植物下胚轴的生长，阐明了 RVE5 协调生物钟与高温下植物生长的竞争-衰减分子机制（Li et al., *New Phytol*, 2022, 刘建祥课题组）。

（二）植物*I*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，发现在水分胁迫下质子泵 AHA2 调控 H^+快速流出保卫细胞，造成细胞质碱化和 ROS 积累，进而响应 ABA 诱导的气孔关闭（Pei et al., *Plant Cell*, 2022, 巩志忠课题组）；阐明了微管结合蛋白 SPR1 调控 ABA 诱导的微管解聚以及气孔关闭的分子功能（Wang et al., *Plant Cell*, 2022, 毛同林、王向锋课题组）；解析了 COP1 通过转录和翻译后水平的双重调控机制，促进 ABA 对 *ABI5* 基因表达和蛋白水平的诱导，从而在黑暗下调控 ABA 信号转导的分子机制（Peng et al., *Plant Cell*, 2022, 李继刚课题组）。

在植物养分高效利用研究方面，揭示了 CIPK1-NAC075 响应低氮胁迫，调控植物根系可塑性生长的分子机制（Xiao et al., *Dev Cell*, 2022, 张静课题组）；阐明了韧皮部质外体铁积累在铵胁迫抑制植物根系生长中的作用机制（Liu et al., *Nat Commun*, 2022, 金崇伟课题组）；解析了钾离子通道 AKT1 的蛋白结构，并阐明了 AKT1 活性调控与构象变化之间的联系（Lu et al., *Nat Commun*, 2022, 武维华、王毅课题组）；发现了类受体蛋白激酶 BAK1 通过调控质子泵活性影响植物钾吸收的分子机制（Wang et al., *Plant Physiol*, 2022, 武维华、王毅课题组）；解析了新型糖转运蛋白 SUGCAR1 调控玉米籽粒灌浆过程中同化产物与矿质养分协同运输的分子机制（Yang et al., *Plant Cell*, 2022, 赖锦盛、王毅课题组）。

在植物光高效利用研究方面，揭示了植物远红光信号途径的两个重要正调控因子 HY5 和 TZP 相互促进、协同调控远红光信号转导的分子机制（Li et al., *Plant Cell*, 2022, 李继刚课题组）；阐明了 14-3-3 蛋白通过促进 PIF3 的磷酸化和降解，调控植物光形态建成的分子机制（Song et al., *New Phytol*, 2023, 李继刚课题组）。

（三）植物*I*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，解析了 SNARE 蛋白 SYP121 作为 ROP2 效应因子调控根毛顶端生长的分子机制（Cui et al., *Mol Plant*, 2022, 傅缨课题组）；揭示了转录因子 HY5 通过微管骨架参与调控侧根发生的分子机制（Qian et al., *Plant Cell*, 2022, 毛同林、王向锋课题组）；揭示了染色质重塑因子 CLASSY 调控植物组织特异性 DNA 甲基化模式的遗传基础（Zhou et al., *Nat Commun*, 2022, 周明课题组）；发现干旱胁迫

下根系微生物物种间的竞争减弱，而正相互作用频率增加，揭示了微生物组抗逆的复杂性（Gao et al., *Nat Commun*, 2022, 徐凌课题组）；阐明了热激蛋白 HSP101 调控玉米花粉母细胞减数分裂抗热性的功能与机制（Li et al., *Plant Cell*, 2022, 金危危课题组）；解析了细胞质转化酶 INVAN6 参与热胁迫下的糖代谢和糖信号调控，进而调控玉米减数分裂的分子机制（Huang et al., *New Phytol*, 2022, 金危危课题组）。

（四）作物抗逆高效的分子设计和种质创新

在作物高产基因发掘方面，克隆了玉米穗行数调控基因 *KRN2* 及水稻二次枝梗数调控基因 *OsKRN2*，解析了 *KRN2* 和 *OsKRN2* 负调控玉米穗行数与水稻枝梗数的分子机制，揭示了 *KRN2* 和 *OsKRN2* 在驯化和改良过程中的演化规律，创制了能增产~10%的 *KRN2*/*OsKRN2* 突变体材料（Chen et al., *Science*, 2022, 杨小红、李建生课题组）。此项研究成果入选 2022 中国十大科技进展新闻，该成果不仅揭示了玉米与水稻的同源基因趋同进化从而增加玉米与水稻产量的机制，为育种提供了宝贵的遗传资源，而且为农艺性状关键控制基因的解析与育种应用，以及其它优异野生植物快速再驯化或从头驯化提供重要理论基础。发现纤维素合成酶 ENB1 是合成玉米基底胚乳传递层细胞壁内突的关键因子，揭示了 ENB1 调控玉米籽粒永久型胚乳形成的分子机制（Wang et al., *Plant Cell*, 2022, 宋任涛课题组）。

在作物抗逆基因挖掘方面，阐明了 bZIP68 转录因子调控玉米耐冷性的分子机制，发现了在耐冷玉米培育中有利用价值的 *bZIP68* 优异等位变异（Li et al., *Plant Cell*, 2022, 杨淑华课题组）；解析了玉米 SOS 途径组分的功能变异导致耐盐性变异的分子遗传基础（Zhou et al., *New Phytol*, 2022, 蒋才富课题组）；发现 ZmHKT1;2 促进玉米地上部 Na^+ 排斥，阐明了该基因优良等位变异的遗传演化规律（Zhang et al., *Plant Biotechnol J*, 2022, 蒋才富课题组）；解析了 ZmSRO1d 调控玉米平衡生长与干旱胁迫应答的机制，揭示了 *ZmSRO1d* 在玉米驯化和现代育种过程中的演化规律（Gao et al., *Mol Plant*, 2022, 秦峰课题组）。

在作物种质创新技术体系建设方面，建立了优化的引导编辑系统 ePEmax，并通过该系统创制了草甘膦抗性水稻（Jiang et al., *Mol Plant*, 2022, 陈其军课题组）；搭建了麦类多维组学数据整合及比较分析平台 WheatCENet（Li et al., *Genom Proteom Bioinf*,

2022，苏震课题组）。上述研究为培育耐逆高产农作物新品种提供了新的理论基础、技术体系和遗传资源。

（五）作物抗逆高效性状的化学调控技术及应用

通过优化氮素管理减少了小麦-玉米轮作系统中活性氮的损失，并获得了最大经济效益，活性氮损耗成本降低 18.4-83.1%，有利于华北平原麦-玉轮作系统的可持续集约化生产（Liu et al., *J Clean Prod*, 2022，李召虎课题组）；阐明了肥料稳定剂通过靶向调节微生物氮转化减少农业土壤中氧化亚氮排放的作用机制（Liu et al., *Sci Total Environ*, 2022，李召虎课题组）；创建了基于星状纳米载体的小 RNA 体外递送系统，并首次应用在玉米上，为开发小 RNA 类植物生长调节剂奠定基础（Yang et al., *J Nanobiotechnol*, 2022，段留生课题组）。

五、发表的重要研究论文

序号	姓名	论文名称	期刊名称	影响因子
1	杨小红	Convergent selection of a WD40 protein that enhances grain yield in maize and rice	*Science*	59.937
2	陈艳梅	Dissecting the plant chromatin interactome using mass spectrometry	*Trends Biotechnol*	20.864
3	陈艳梅	Mapping histone modification-dependent protein interactions with chemical proteomics	*Trends Biochem Sci*	20.792
4	巩志忠	RAF22, ABI1 and OST1 form a dynamic interactive network that optimizes plant growth and responses to drought stress in *Arabidopsis*	*Mol Plant*	19.617
5	傅　缨	*Arabidopsis* SYP121 acts as an ROP2 effector in the regulation of root hair tip growth	*Mol Plant*	19.617
6	秦　峰	Natural variations of ZmSRO1d modulate the trade-off between drought resistance and yield by affecting ZmRBOHC-mediated stomatal ROS production in maize	*Mol Plant*	19.617
7	陈其军	Optimized prime editing efficiently generates glyphosate-resistant rice plants carrying homozygous TAP-IVS mutation in EPSPS	*Mol Plant*	19.617
8	杨淑华	Natural polymorphism of ZmICE1 contributes to amino acid metabolism that impacts cold tolerance in maize	*Nat Plants*	19.328
9	周　明	The CLASSY family controls tissue-specific DNA methylation patterns in *Arabidopsis*	*Nat Commun*	17.764
10	蒋才富	A dirigent family protein confers variation of Casparian strip thickness and salt tolerance in maize	*Nat Commun*	17.764
11	金崇伟	Phloem iron remodels root development in response to ammonium as the major nitrogen source	*Nat Commun*	17.764
12	杨淑华 丁杨林	CPK28-NLP7 module integrates cold-induced Ca^{2+} signal and transcriptional reprogramming in *Arabidopsis*	*Sci Adv*	16.9
13	杨淑华 丁杨林	Surviving and thriving: How plants perceive and respond to temperature stress	*Dev Cell*	13.294
14	张　静	Nitrate availability controls translocation of the transcription factor NAC075 for cell type-specific reprogramming of root growth	*Dev Cell*	13.294
15	李继刚	Mutual upregulation of HY5 and TZP in mediating phytochrome A signaling	*Plant Cell*	12.796
16	宋任涛	ENB1 encodes a cellulose synthase 5 that directs synthesis of cell wall ingrowths in maize basal endosperm transfer cells	*Plant Cell*	12.796
17	巩志忠	Phosphorylation of the plasma membrane H^+-ATPase AHA2 by BAK1 is required for ABA-induced stomatal closure in *Arabidopsis*	*Plant Cell*	12.796

序号	姓名	论文名称	期刊名称	影响因子
18	李继刚	COP1 positively regulates ABA signaling during *Arabidopsis* seedling growth in darkness by mediating ABA-induced ABI5 accumulation	*Plant Cell*	12.796
19	杨淑华 施怡婷	The transcription factor bZIP68 negatively regulates cold tolerance in maize	*Plant Cell*	12.796
20	陈立群	*Arabidopsis* ERdj3B coordinates with ERECTA-family receptor kinases to regulate ovule development and the heat stress response	*Plant Cell*	12.796
21	金危危	Heat shock protein 101 contributes to the thermotolerance of male meiosis in maize	*Plant Cell*	12.796
22	赖锦盛 王　毅	The sugar transporter ZmSUGCAR1 of the nitrate transporter 1/peptide transporter family is critical for maize grain filling	*Plant Cell*	12.796
23	郭　岩	SALT OVERLY SENSITIVE 1 is inhibited by clade D protein phosphatase 2C D6 and D7 in *Arabidopsis thaliana*	*Plant Cell*	12.796
24	王向锋	The OPEN STOMATA1–SPIRAL1 module regulates microtubule stability during abscisic acid-induced stomatal closure in *Arabidopsis*	*Plant Cell*	12.796
25	毛同林 王向锋	HY5 inhibits lateral root initiation in *Arabidopsis* through negative regulation of the microtubule-stabilizing protein TPXL5	*Plant Cell*	12.796
26	田　丰	Plant genetics: Mechanisms of wild soybean adaptation	*Curr Biol*	12.621
27	蒋才富	A teosinte-derived allele of an HKT1 family sodium transporter improves salt tolerance in maize	*Plant Biotechnol J*	11.619
28	段留生	Construction and application of star polycation nanocarrier-based microRNA delivery system in *Arabidopsis* and maize	*J Nanobiotechnol*	11.509
29	张明才	Optimizing nitrogen management diminished reactive nitrogen loss and acquired optimal net ecosystem economic benefit in a wheat-maize rotation system	*J Clean Prod*	11.016
30	傅　缨	ECAP is a key negative regulator mediating different pathways to modulate salt stress-induced anthocyanin biosynthesis in *Arabidopsis*	*New Phytol*	10.768
31	蒋才富	The classical SOS pathway confers natural variation of salt tolerance in maize	*New Phytol*	10.768
32	刘建祥	A competition-attenuation mechanism modulates thermoresponsive growth at warm temperatures in plants	*New Phytol*	10.768
33	李继刚	14-3-3 proteins regulate photomorphogenesis by facilitating light-induced degradation of PIF3	*New Phytol*	10.768
34	金危危	Maize cytosolic invertase INVAN6 ensures faithful meiotic progression under heat stress	*New Phytol*	10.768

序号	姓名	论文名称	期刊名称	影响因子
35	张明才	Fertilizer stabilizers reduce nitrous oxide emissions from agricultural soil by targeting microbial nitrogen transformations	*Sci Total Environ*	10.237
36	苏　震	WheatCENet: a database for comparative co-expression networks analysis of allohexaploid wheat and its progenitors	*Genom Proteom Bioinf*	10.196
37	傅　缨	The transcription factor ZmMYB69 represses lignin biosynthesis by regulating ZmMYB31 and ZmMYB42 in maize	*Plant Physiol*	9.115
38	王　毅	Receptor-like protein kinase BAK1 promotes K^+ uptake by regulating H^+-ATPase AHA2 under low potassium stress	*Plant Physiol*	9.115
39	朱　蕾	Stable ARMADILLO REPEAT KINESIN 2 in light inhibits hypocotyl elongation and facilitates light-induced cortical microtubule reorientation in *Arabidopsis*	*J Exp Bot*	8.331
40	周文焜	Small bending, big curvature	*J Integr Plant Biol*	8.241
41	李继刚 杨淑华	Integration of light and temperature signaling pathways in plants	*J Integr Plant Biol*	8.241
42	杨永青	Testing the polar auxin transport model with a selective plasma membrane H^+-ATPase inhibitor	*J Integr Plant Biol*	8.241
43	丁忠杰	RING-box proteins regulate leaf senescence and stomatal closure via repression of ABA transporter gene ABCG40	*J Integr Plant Biol*	8.241
44	杨建立	The miR157-SPL-CNR module acts upstream of bHLH101 to negatively regulate iron deficiency responses in tomato	*J Integr Plant Biol*	8.241
45	巩志忠	BAK1 plays contrasting roles in regulating abscisic acid‐induced stomatal closure and abscisic acid inhibited primary root growth in *Arabidopsis*	*J Integ Plant Biol*	8.241
46	刘建祥	UBA domain protein SUF1 interacts with NatA-complex subunit NAA15 to regulate thermotolerance in *Arabidopsis*	*J Integr Plant Biol*	8.241
47	刘建祥	REVEILLE 7 inhibits the expression of the circadian clock gene EARLY FLOWERING 4 to fine-tune hypocotyl growth in response to warm temperatures	*J Integr Plant Biol*	8.241
48	杨建立	Abscisic acid-dependent PMT1 expression regulates salt tolerance by alleviating abscisic acid-mediated reactive oxygen species production in *Arabidopsis*	*J Integr Plant Biol*	8.241
49	朱　蕾	ARK2 stabilizes the plus-end of microtubules and promotes microtubule bundling in *Arabidopsis*	*J Integr Plant Biol*	8.241
50	陈其军	Optimized prime editing efficiently generates heritable mutations in maize	*J Integr Plant Biol*	8.241
51	苏　震	KNOX II transcription factor HOS59 functions in regulating rice grain size	*Plant J*	8.028

序号	姓名	论文名称	期刊名称	影响因子
52	郑绍建	A novel kinase subverts aluminum resistance by boosting Ornithine decarboxylase-dependent putrescine biosynthesis	*Plant Cell Envrion*	7.947
53	寿惠霞	Functional characterization of the three Oryza sativa SPX-MFS proteins in maintaining phosphate homeostasis	*Plant Cell Envrion*	7.947
54	莫肖蓉	Characterizing membrane anchoring of leaf-form ferredoxin-NADP$^+$ oxidoreductase in rice	*Plant Cell Envrion*	7.947
55	刘建祥	The FtsH-inactive protein FtsHi5 is required for chloroplast development and protein accumulation in chloroplasts at low ambient temperature in *Arabidopsis*	*Front Plant Sci*	7.255
56	杨建立	Potential role of domains rearranged methyltransferase7 in starch and chlorophyll metabolism to regulate leaf senescence in tomato	*Front Plant Sci*	7.255
57	杨建立	The tomato transcription factor slnac063 is required for aluminum tolerance by regulating slaae3-1 expression	*Front Plant Sci*	7.255
58	王智烨	Probing in vivo RNA structure with optimized DMS-MaPseq in rice	*Front Plant Sci*	7.255
59	徐　娟	Regulation of *Arabidopsis* matrix metalloproteinases by mitogen-activated protein kinases and their function in leaf senescence	*Front Plant Sci*	7.255
60	陈益芳	The ubiquitin E3 ligase PRU2 modulates phosphate uptake in *Arabidopsis*	*Int J Mol Sci*	6.628
61	张学琴	MAP3Kε1/2 interact with MOB1A/1B and play important roles in control of pollen germination through crosstalk with JA signaling in *Arabidopsis*	*Int J Mol Sci*	6.628
62	王　毅	STOP1 regulates LKS1 transcription and coordinates K^+/$NH4^+$ balance in *Arabidopsis* response to low-K^+ stress	*Int J Mol Sci*	6.628
63	刘建祥	Regulation of chloroplast development and function at adverse temperatures in plants	*Plant Cell Physiol*	5.783
64	杨小红	Identifying QTL and candidate genes for prolificacy in maize	*Crop J*	5.781
65	金危危	Amino acid permease 6 regulates grain protein content in maize	*Crop J*	5.781
66	杨小红	Population genomics of *Zea* species identifies selection signatures during maize domestication and adaptation	*BMC Plant Biology*	5.761
67	刘凤霞	Polyamine oxidase 3 is involved in salt tolerance at the germination stage in rice	*JGG*	5.224
68	李　岩	AtFTCD-L, a trans-Golgi network localized protein, modulates root growth of *Arabidopsis* in high-concentration agar culture medium	*Planta*	4.689

序号	姓名	论文名称	期刊名称	影响因子
69	段留生	Design, synthesis and herbicidal evaluation of novel urea derivatives with inhibition activity to root growth	*J Plant Growth Regul*	4.469
70	苏　震	Systems biology-based analysis indicates that PHO1;H10 positively modulates high light-induced anthocyanin biosynthesis in *Arabidopsis* leaves	*Genomics*	4.38

累计 SCI 影响因子 805，平均影响因子 11.5/篇。

植物生理学与生物化学国家重点实验室

State Key Laboratory of Plant Physiology and Biochemistry

http://sklppb.cau.edu.cn/

六、获得的发明专利和软件著作权

序号	姓名	专利号	成果名称	授权公告日
1	巩志忠	ZL202010930137.2	玉米 *CPK2* 基因在植物抗旱中的应用	2022.02.08
2	李召虎	US11242537B2	Method for improving sensitivity of plant to gibberellin inhibitor and use thereof	2022.02.08
3	孙传清	JP7023979	タンパク質 nog1 の植物仅量と一穂粒数の調節への応用	2022.02.14
4	蒋才富	ZL202110223406.6	一种玉米耐受盐胁迫导致的渗透胁迫的基因、分子标记和应用	2022.04.05
5	王　瑜	ZL201911417842.6	PP84 蛋白及其编码基因在调控植物抗旱性中的应用	2022.04.05
6	秦　峰	ZL201910160207.8	蛋白 ZmTIP1 在调控植物抗旱性中的应用	2022.04.05
7	金危危	ZL201910602376.2	蛋白质 HEI10 在调控玉米产量和抗病性中的应用	2022.04.05
8	巩志忠	ZL202011003964.3	DRK 蛋白及其编码基因在植物抗旱中的应用	2022.04.12
9	郑绍建	ZL202010973235.4	一种拟南芥种子铁累积调控基因 INO 及其编码蛋白和应用	2022.04.15
10	苏　震	ZL201911323001.9	拟南芥 PHO1；H10 蛋白及其编码基因在调控植物叶片花青素合成中的应用	2022.04.26
11	徐明良	ZL201910160206.3	一种培育抗灰斑病植物的方法	2022.05.10
12	王　瑜	ZL202011005398.X	GLK7 蛋白及其编码基因在植物抗旱中的应用	2022.05.17
13	毛传澡	ZL202110194477.8	水稻根分泌多肽 PEP1 及其编码基因和应用	2022.05.27
14	毛传澡	ZL202011618909.5	OsWRKY12 及其在水稻磷高效育种中的应用	2022.05.27
15	毛传澡	ZL202011591443.4	一种蛋白磷酸酶 OsPP74 在提高水稻磷吸收中的应用	2022.06.10
16	蒋才富	ZL202010771030.8	一种玉米抗盐主效 QTL 基因及其应用	2022.06.14
17	寿惠霞	ZL202110526546.0	pSOY19-ZM2 载体、其制备方法及应用	2022.06.27
18	郑绍建	ZL202110367334.2	一种调控植物抗铝性的铝离子受体 ALR1 基因或蛋白的应用	2022.07.08
19	杨淑华	ZL201911325467.2	ZmbZIP68 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用	2022.07.15
20	田　丰	ZL201910496614.6	玉米基因 *ZmRAVL1* 和功能位点及其用途	2022.07.15
21	杨淑华	ZL201911319236.0	玉米耐低温基因 *ZmCIPK10.1* 在提高植物耐寒性中的应用	2022.07.19
22	陈其军	ZL201910890027.5	用于植物基因编辑的成套载体及其应用	2022.08.09

序号	姓名	专利号	成果名称	授权公告日
23	段留生	ZL202110757356.X	一种调节植物生长的组合物及其制备方法与应用	2022.08.09
24	段留生	ZL202110757950.9	一种调节棉花株型提高抗逆性的组合物及其制备方法与应用	2022.08.09
25	金危危	ZL201910387858.0	蛋白质 INVAN6、其编码基因以及它们在选育玉米雄性不育系中的应用	2022.08.09
26	李召虎	ZL202010985865.3	棉花丝/苏氨酸蛋白磷酸酶 GhTOPP6 及其编码基因和应用	2022.08.16
27	杨淑华	ZL201911402494.5	玉米 MYB39 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用	2022.09.06
28	杨淑华	ZL201911421824.5	玉米 CRR1 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用	2022.09.06
29	田晓莉	ZL202110283930.2	棉花钾离子通道蛋白 GhAKT2 及其编码基因和应用	2022.09.16
30	任东涛	ZL201810058730.5	玉米 ZmMPK11 蛋白或其编码基因在调节植物耐逆性中的应用	2022.09.16
31	刘建祥	ZL202111098837.0	时钟基因 *RVE5* 在调控植物生长和开花时间中的应用	2022.10.08
32	陈益芳	ZL201910422464.4	蛋白 PNR1 在培育磷营养高效植物品种中的应用	2022.11.01
33	陈丽梅	ZL202010143364.0	ZmbHLH148 蛋白及其编码基因在调控植物抗旱性中的应用	2022.11.22
34	程金魁	2022SR1443183	转基因玉米全流程数据管理系统 V1.0	2022.11.01

七、承担的主要研究项目

（一）纵向研究项目

序号	姓名	项目（课题）编号	项目（课题）名称	项目来源	起止时间
1	郭　岩	31921001	植物非生物迫感受和应答	基金委	2020.01-2024.12
2	王　毅	32025004	植物感受低钾胁迫的分子机理	基金委	2021.01-2025.12
3	田　丰	32025027	玉米驯化与适应的分子遗传基础	基金委	2021.01-2025.12
4	李继刚	32225006	植物光信号转导	基金委	2023.01-2027.12
5	杨小红	32225036	玉米重要产量与品质性状的遗传基础	基金委	2023.01-2027.12
6	徐　娟	31922005	植物信号转导	基金委	2020.01-2022.12
7	施怡婷	32022008	植物低温胁迫应答	基金委	2021.01-2023.12
8	张　静	32022007	植物/作物根系可塑性生长发育	基金委	2021.01-2023.12
9	郑绍建	31730006	一个颠覆植物铝敏感性的类受体激酶的功能解析	基金委	2018.01-2022.12
10	巩志忠	31730007	类受体蛋白激酶 GHR1 介导气孔运动的分子机理	基金委	2018.01-2022.12
11	杨淑华	31730011	蛋白磷酸酶 CRPPs 调控植物感受和应答低温信号的分子机制	基金委	2018.01-2022.12
12	宋任涛	31730065	玉米醇溶蛋白转录因子 *Opaque2* 的翻译后修饰调控研究	基金委	2018.01-2022.12
13	孙传清	31830065	栽培稻驯化过程中穗粒数增加的分子机理研究	基金委	2019.01-2023.12
14	徐明良	31930082	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	基金委	2019.10-2024.12
15	李召虎	31930079	棉花化控栽培分子机制及轻简作物构建研究	基金委	2020.01-2024.12
16	巩志忠	32030008	钙信号调控玉米抗旱的分子机制研究	基金委	2021.01-2025.12
17	郭　岩	32130007	盐胁迫下植物根系生长发育 调控的分子机制	基金委	2022.01-2026.12
18	孙传清	32130079	水稻驯化过程中丰产性与适应性协同改良的分子机制研究	基金委	2022.01-2026.12
19	杨淑华	31920103002	Ca^{2+}信号参与植物低温胁迫应答的分子调控机制研究	基金委	2020.01-2024.12
20	傅　缨	32061143018	细胞表面的信号传递-ROP GTPases 调控通路在细胞极性及生长过程中的功能机制研究	基金委	2020.10-2023.09

序号	姓名	项目（课题）编号	项目（课题）名称	项目来源	起止时间
21	王　毅	32161133014	植物感受和适应低钾胁迫的分子机制	基金委	2022.01-2024.12
22	李召虎	32120103008	Mn_3O_4 纳米拟酶提高棉花抗旱性的生理分子机制	基金委	2022.01-2026.12
23	陈其军	U19A2022	DNA 甲基化和分化控制基因影响江淮地区籼稻碱基编辑的分子机制解析及应用	基金委	2020.01-2023.12
24	徐明良	U2004205	玉米广谱抗穗粒腐病基因的克隆及遗传机制解析	基金委	2021.01-2024.12
25	蒋才富	U2106229	玉米木质部 Na^+卸载的分子机制及其在耐盐种质创新中的应用	基金委	2021.01-2025.12
26	王　瑜	32070308	转录因子 *ZmAL14* 在调节玉米干旱胁迫响应中的作用	基金委	2021.01-2024.12
27	张明才	31871546	ZmNPFs 和 ZmNRT2.1 调节玉米根系氮素吸收的乙烯信号应答及其调控机制	基金委	2019.01-2022.12
28	王向锋	31872644	微管结合蛋白 WDL4 调控囊泡运输参与顶端弯钩细胞生长的分子机理	基金委	2019.01-2022.12
29	刘建祥	31872653	拟南芥 PPR 蛋白 TSL1 协调温度信号与叶绿体发育的分子机理	基金委	2019.01-2022.12
30	施怡婷	31872658	光信号转录因子 PIF 调控植物低温应答的分子机制	基金委	2019.01-2022.12
31	杨永青	31872659	植物质膜 H^+-ATPase 活性“自抑制”状态维持及解除的分子机制	基金委	2019.01-2022.12
32	傅　缨	31872662	拟南芥 JEM 蛋白在茉莉素调控花青素合成信号转导中的作用机制研究	基金委	2019.01-2022.12
33	陈立群	31872668	拟南芥 *SVL4* 和 *SVL5* 基因调控花粉管细胞壁合成的分子机制	基金委	2019.01-2022.12
34	陈其军	31872678	*CRISPR/Cas* 基因组编辑和碱基编辑技术在玉米中的高通量应用研究	基金委	2019.01-2022.12
35	毛同林	31872821	微丝封端蛋白 capping protein 参与植物响应盐胁迫的分子机制	基金委	2019.01-2022.12
36	李继刚	31970262	转录因子 *PIFs* 调控植物 ABA 信号途径的分子机理研究	基金委	2020.01-2023.12
37	丁忠杰	31970272	植物响应铝毒的上游重要信号组件挖掘及其功能解析	基金委	2020.01-2023.12
38	陈益芳	31970273	转录因子 PNR1 在低磷胁迫条件下调控拟南芥和玉米氮磷吸收的分子机制	基金委	2020.01-2023.12
39	任东涛	31970276	拟南芥鞘脂合成关键限速酶丝氨酸-棕榈酰转移酶（SPT）的 AtLCB1 亚基磷酸化及磷酸化对 SPT 功能调控的机理研究	基金委	2020.01-2023.12

序号	姓名	项目（课题）编号	项目（课题）名称	项目来源	起止时间
40	丁杨林	31970295	E3 泛素连接酶 PUBa/b 调控拟南芥耐冻性的分子机制	基金委	2020.01-2023.12
41	张学琴	31970337	拟南芥蛋白激酶 ZDK 与 ZMP1 共同调控花粉萌发时间进程机制的研究	基金委	2020.01-2023.12
42	苏　震	31970629	基于多组学分析探索植物核纤层类似蛋白影响染色质状态和基因表达的动态调控规律	基金委	2020.01-2023.12
43	田　丰	31971892	解析玉米驯化中代谢分化的遗传基础	基金委	2020.01-2023.12
44	金危危	31971949	一个新的玉米显性花器官发育缺陷基因克隆与功能分析	基金委	2020.01-2023.12
45	秦　峰	31971952	玉米硫酰基转移酶基因在促进根毛伸长和抗旱性中的作用	基金委	2020.01-2023.12
46	毛传澡	31972486	缺磷诱导转录因子的功能及分子调控机制	基金委	2020.01-2023.12
47	杨永青	32070301	类受体激酶 GSO1 响应盐胁迫的分子机制研究	基金委	2021.01-2024.12
48	李　媛	32070310	拟南芥 MPK3/MPK6 介导的细胞壁应答盐胁迫机制研究	基金委	2021.01-2024.12
49	朱　蕾	32070311	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	基金委	2021.01-2024.12
50	周文焜	32070874	植物 RBR 蛋白网络调控根尖干细胞损伤修复的分子机制	基金委	2021.01-2024.12
51	张明才	32071920	赤霉素与 ZmNRT2.1 互作调控玉米根系氮素吸收的机制研究	基金委	2021.01-2024.12
52	蒋才富	32071933	ZmSTL1 调控玉米内皮层凯氏带发育，促进抗盐的分子机制	基金委	2021.01-2024.12
53	王智烨	32170262	拟南芥染色质重塑蛋白 CHR2 的 RNA 结构重塑功能研究	基金委	2022.01-2025.12
54	张　静	32170265	转录因子 *LNRM2* 响应低氮胁迫调控植物根生长发育的分子机制	基金委	2022.01-2025.12
55	王良省	32170284	叶绿体蛋白 SAFE1 和 SAFE2 介导单线态氧信号转导的机理研究	基金委	2022.01-2025.12
56	苏　震	32170673	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	基金委	2022.01-2025.12
57	毛同林	32170682	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	基金委	2022.01-2025.12
58	刘升学	32171940	玉米 Reticulons 家族蛋白基因 *ZmRB16* 调控玉米抗旱性的功能研究	基金委	2022.01-2025.12
59	刘凤霞	32171968	普通野生稻苗期耐冷基因 *LTTS9* 的克隆及功能研究	基金委	2022.01-2025.12
60	杨志蕊	32101657	*ZmAGO4* 调控玉米响应干旱胁迫的分子机制	基金委	2022.01-2024.12

序号	姓名	项目（课题）编号	项目（课题）名称	项目来源	起止时间
61	李召虎	2018YFD1000903	大田经济作物逆境生理及调控	科技部	2018.07-2022.12
62	杨淑华	2020YFA0509902	蛋白复合物调控温度信号转导的机理研究	科技部	2020.12-2025.11
63	王　毅	2021YFF1000502	玉米磷、钾高效利用性状形成的分子调控网络	科技部	2021.12-2026.11
64	毛传澡	2021YFF1000402	水稻小麦磷钾高效利用性状形成的分子调控网络	科技部	2021.12-2026.11
65	杨志蕊	2021YFD1200703-5	玉米抗逆种质资源精准鉴定与优异等位基因挖掘	科技部	2021.12-2026.11
66	王　毅	2021YFF1000500	玉米、大豆等作物养分高效利用性状形成的分子调控网络	科技部	2021.12-2026.11
67	寿惠霞	2021YFF1001204	大豆产量和品质协同调控分子网络	科技部	2021.12-2024.12
68	刘建祥 吴忠长	2021YFF1000404	适应土壤环境的水稻小麦养分高效和高产潜力协同机制	科技部	2021.12-2026.11
69	莫肖蓉 徐纪明	2021YFF1000403	水稻根系发育和养分高效的研究	科技部	2021.12-2026.11
70	刘建祥	2022YFF1001603	粮食作物响应低高温与低光胁迫的遗传与分子调控网络	科技部	2022.12-2027.11
71	周文焜	1021-62332005	植物适应胁迫信号的干细胞调控机理	教育部中组部	2021.01-2023.12
72	秦　峰	BJJWZYJH012019100019026	北京高等学校卓越青年科学家项目	北京市	2019.09-2024.09
73	田晓莉	CARS-15-16	现代农业产业技术体系-棉花-化学调控	农业农村部	2022.01-2025.12
74	杨小红	2018B020202008	优质，多抗，适宜轻简化栽培甜玉米新品种选育	广东省科学技术厅	2018.11-2022.12
75	杨志蕊	2022TC142	干旱胁迫导致玉米雌雄穗发育不协调的机制研究	教育部	2022.01-2022.12
76	王良省	15052023	叶绿体抗氧化胁迫及光能高效利用的分子机理	中国农业大学	2020.01-2025.12
77	赖锦盛	2022010202-3	高产多抗宜机收玉米种质关键性状基因挖掘	省部级	2022.04-2023.12
78	赖锦盛	21ZD10NF003 -1	玉米新型核不育制种技术研究	省部级	2022.01-2024.12
79	郑绍建	NT2021010	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	岭南现代农业科学与技术广东省实验室	2021.01-2023.12
80	刘建祥	LD21C020001	耐高温水稻精准设计育种的分子基础与种质创新	浙江省基金委	2021.01-2023.12
81	王智烨	LZ22C150002	新型 RNA 靶向的 CRISPR/Cas13b 在水稻缺磷胁迫响应研究中的应用	浙江省基金委	2022.01-2024.12
82	金崇伟	LZ21D010001	铵硝化阻抑措施减控蔬菜镉污染的作用，机理及技术优化研究	浙江省基金委	2021.01-2023.12

序号	姓名	项目（课题）编号	项目（课题）名称	项目来源	起止时间
83	王智烨	LZ22C150002	新型 RNA 靶向的 CRISPR/Cas13b 在水稻缺磷胁迫响应研究中的应用	浙江省基金委	2022.01-2024.12
84	莫肖蓉	LZ21C020002	探索植物 *TROL2* 基因的功能及进化演变	浙江省基金委	2021.01-2023.12
85	周　明	LZ22C020001	低温调控硼代谢影响水稻穗发育的分子机制	浙江省基金委	2022.01-2024.12
86	丁忠杰	LY21C020001	乙烯信号转导新调控因子的鉴定及其功能研究	浙江省基金委	2021.01-2023.12
87	刘建祥	2019R52005	植物逆境生物学	浙江省科技厅	2020.01-2022.12
88	陈丽梅	B21HJ0503	玉米氮素高效利用基因的挖掘和种质创新	崖州湾种子实验室	2021.12-2024.11
89	王良省	31051102	生物学一流学科科研协同创新项目	中国农业大学	2022.01-2022.12

（二）自主研究项目

序号	申请人	课题名称	资助额度（万元）
1	杨淑华	小肽 CIP1-类受体激酶 CRIK1 模块感知低温信号的分子机制	35
2	田　丰	玉米耐密株型的分子调控网络	38
3	郭　岩	类受体激酶 GSO1 参与调控植物耐盐性的分子机制	35
4	巩志忠	玉米抗旱功能基因解析	28
5	宋任涛	玉米籽粒发育中逆境响应的分子机制研究	25
6	孙传清	野生稻苗期耐冷基因 *CTS12* 的克隆与功能研究	45
7	李继刚	*COP1* 在黑暗下调控植物 ABA 信号途径的分子机制研究	28
8	王　毅	钙调素蛋白 ZmCaM 调控玉米细胞钾动态平衡的机制研究	20
9	徐明良	细胞壁相关激酶 ZmWAK-RLK 介导的玉米灰斑病抗性机制研究	20
10	蒋才富	ZmSDT1 介导的玉米抗盐、抗旱共性分子机制解析	23
11	陈益芳	激酶 SnRK 在植物磷营养和逆境应答交叉网络中的分子调控机制	20
12	秦　峰	干旱逆境胁迫诱导玉米散粉吐丝间隔的分子机制	18
13	金危危	玉米温敏无雄穗基因 *Tvt2* 的克隆及功能分析	15
14	任东涛	一类新发现的激酶 MAPK-like 的激活方式及调控玉米响应干旱和盐胁迫的机制研究	15
15	陈其军	应用 Prime editing 技术实现作物重要抗逆基因的定向进化	15
16	毛同林	微管骨架参与高温诱导下胚轴细胞生长的机制研究	18
17	段留生	冠菌素调控玉米抗逆防倒的分子机制	15
18	杨小红	玉米穗行数 QTL-*qKRN2* 的克隆及高产等位基因的创制	18
19	傅　缨	拟南芥 JAZ8 介导 JA 信号途径调控盐胁迫响应的分子机制研究	13
20	赖锦盛	奖励支持	20
21	王良省	引进人才支持	10
22	周文焜	引进人才支持	10
23	徐　凌	引进人才支持	10

八、国内外学术交流

（一）邀请国内外同行讲学

序号	邀请人	被邀请报告人姓名、职务	报告人单位	报告题目	报告日期
1	杨淑华	瞿礼嘉，教授	北京大学	植物雌雄互作调控受精的分子机制	2022.03.03
2	杨淑华	王佳伟，研究员	中科院分子植物科学卓越中心	植物时序性发育与生命周期	2022.03.10
3	杨淑华	夏光敏，教授	山东大学	黄河三角洲小麦耐逆育种研究	2022.03.24
4	杨淑华	王二涛，研究员	中科院分子植物科学卓越创新中心	植物-微生物共生与营养吸收	2022.03.31
5	杨淑华	杨小红，教授	中国农业大学	殊途同归：玉米和水稻趋同选择的奥秘	2022.04.06
6	杨淑华	刘玉乐，教授	清华大学	木尔坦棉花曲叶病毒致病的分子机制	2022.04.07
7	杨淑华	白明义，教授	山东大学	油菜素甾醇调控植物环境适应性的分子机制	2022.04.14
8	杨淑华	何跃辉，教授	北京大学	“春化作用”的表观遗传调控机制	2022.04.28
9	杨淑华	周传恩，教授	山东大学	苜蓿复叶发育的分子机制研究	2022.05.12
10	杨淑华	杨元合，研究员	中国科学院植物研究所	高寒草地碳氮循环对冻土融化的响应	2022.05.19
11	杨淑华	Brigitte Poppenberger，教授	德国慕尼黑工业大学	An expanded model of heat stress signaling - how brassinosteroids take part	2022.07.27
12	杨淑华	Michael John Holdsworth，教授	英国诺丁汉大学	The role of oxygen-sensing in plant environmental adaptation	2022.07.27
13	蒋才富	Sergey Shabala，教授	澳大利亚塔斯玛尼亚大学	Membrane transporters in sensing and signalling of soil salinity and hypoxia	2022.07.27
14	巩志忠	Hannes Kollist，教授	爱沙尼亚塔尔图大学	Stomatal regulation by the environment	2022.07.27
15	王良省	Chanhong Kim，研究员	中国科学院分子植物科学卓越创新中心	Progressive report about EXECUTER-mediated singlet oxygen signaling	2022.07.27
16	王良省	Jesse Woodson，副教授	美国亚历桑那大学	Chloroplast stress signals and the control of organelle degradation and cell death	2022.07.27

序号	邀请人	被邀请报告人姓名、职务	报告人单位	报告题目	报告日期
17	傅　缨	Miguel Botella，教授	西班牙马拉加大学	A family of peripheral membrane proteins safeguards cellulose synthases during stress adaptation	2022.07.28
18	李继刚	Carlos L. Ballare，教授	阿根廷布宜诺斯艾利斯大学	Growth-defense tradeoffs in plants: concepts and mechanisms involving phytochrome and jasmonate signaling	2022.07.28
19	李继刚	Andreas Hiltbrunner，教授	德国弗莱堡大学	Molecular mechanisms and evolution of phytochrome signalling	2022.07.28
20	田　丰	James Schnable，教授	美国内布拉斯加大学林肯分校	Genes controlling phenotypic variation across environment and time	2022.07.28
21	杨淑华	Hao Yu，院士	新加坡国立大学	RNA modification underlies plant development and stress responses	2022.07.28
22	周文焜	Yusaku Uga，教授	日本国立农业与食品产业技术综合研究机构	Root design: Towards the development of climate-resilient crops	2022.07.29
23	巩志忠	Jian-Kang Zhu，院士	南方科技大学	CRISPR/Cas technologies for breeding, diagnostics and therapeutics	2022.07.29
24	王良省	Dario Leister，院士	德国慕尼黑大学	Enhancing/improving photosynthesis: how it could work – how it does not work	2022.07.29
25	王良省	Paul Javis，教授	英国牛津大学	Ubiquitin-dependent chloroplast-associated protein degradation in plants	2022.07.29
26	杨淑华	Jia Li，教授	广州大学	Root hydrotropism response in *Arabidopsis*	2022.07.29
27	徐　凌	Devin Coleman-Derr，教授	美国加州大学伯克利分校	Host mediated microbiome engineering for selection of beneficial plant microbiomes	2022.07.30
28	徐　凌	Mary Lou Guerinot，教授	美国达特茅斯学院	Shining light on iron deficiency signaling in *Arabidopsis*	2022.07.30
29	郭　岩	Dae-Jin Yun，教授	韩国建国大学	Inverse regulation of SOS1 and HKT1 protein localization and stability by SOS3/CBL4 in *Arabidopsis thaliana*	2022.07.30
30	王智烨	丁一倧，研究员	英国约翰英纳斯研究中心	RNA structure, a hidden regulator in living cells	2022.09.07

序号	邀请人	被邀请报告人姓名、职务	报告人单位	报告题目	报告日期
31	秦　峰	李霞，教授	华中农业大学	大豆与根瘤菌共生结瘤与根瘤数量调控机制研究进展	2022.09.16
32	秦　峰	周奕华，研究员	中国科学院遗传与发育研究所	植物的“精准制造业”：细胞壁生物合成	2022.09.23
33	秦　峰	李乐攻，教授	首都师范大学	基于离子通道组装的分子开关编码植物细胞钙信号	2022.10.14
34	秦　峰	胡玉欣，研究员	中国科学院植物研究所	植物细胞全能性的分子调控	2022.10.21
35	秦　峰	李青，教授	华中农业大学	玉米籽粒发育的遗传与表观遗传调控	2022.10.28
36	秦　峰	姜里文，教授	香港中文大学	Organelle biogenesis and function in plant: copii and vacuole	2022.11.04
37	秦　峰	杨文强，研究员	中国科学院植物研究所	衣藻叶绿体与光合作用	2022.11.11
38	秦　峰	王海洋，教授	华南农业大学	玉米耐密理想株型遗传调控与杂种优势机理解析	2022.11.18
39	宋任涛	刘巧泉，副校长	扬州大学农学院	水稻优质育种的分子基础	2022.11.20
40	宋任涛	赵涵，所长	江苏农科院种质资源与生物技术所	玉米氮吸收遗传调控解析	2022.11.20
41	秦　峰	许操，研究员	中国科学院遗传与发育研究所	植物干细胞调控与设计育种	2022.11.25
42	寿惠霞	Stanton Gelvin，教授	美国普渡大学	Understanding and manipulating the process of agrobacterium T-DNA integration into the plant genome	2022.11.28

（二）在国内外参加会议报告

序号	报告人	报告题目	会议名称	会议时间
1	杨淑华	Cold signaling regulated by phosphorylation in *Arabidopsis*	The 32nd international conference on *Arabidopsis* research（ICAR）	2022. 06.20
2	杨淑华	Molecular regulation of cold tolerance in *Arabidopsis* and maize	New phytologist next generation scientists' 2022（线上）	2022. 07.19
3	杨小红	玉米和水稻趋同选择的遗传规律	首届“植物科学前沿学术大会”	2022.07.18
4	傅　缨	AUGMIN complex in plants	北京地区细胞骨架专题研讨会	2022.08.04
5	杨小红	Convergent selection of a WD40 protein that enhances grain yield in maize and rice	第二十一届全国植物基因组大会	2022.08.19
6	李继刚	Light control of plant response to abiotic stress	2022 植物分子细胞与发育生物学研讨会	2022.08.19
7	李继刚	Light control of plant response to abiotic stress	2022 年“植物逆境适应性”青年论坛	2022.08.25
8	王智烨	植物体内 RNA 结构功能	宁波大学植物病毒研究所“青年学术论坛”	2022.09.02
9	齐俊生	维大力机理研究与产品应用	第 29 届中国杨凌高新科技成果博览会	2022.09.15
10	杨小红	玉米增产基因 *KRN2* 的克隆与育种应用	2022 年全国玉米遗传育种学术研讨会	2022.09.16
11	李继刚	光调控植物逆境响应的分子机制	中国植物生理与植物分子生物学学会 2022 年全国学术年会	2022.09.27
12	王良省	Safeguard chloroplasts from singlet oxygen-induced signaling	CSPB2022 年福州年会	2022.09.27
13	杨淑华	Phosphorylation regulation of cold tolerance in *Arabidopsis*	2022 年亚洲及大洋洲生化大会（线上）	2022.10.19
14	杨淑华	Molecular and genetic basis of cold tolerance in maize	MPlant 植物科学前沿交叉论坛（线上）	2022.10.20
15	郑绍建	植物铁吸收和累积的分子机制	第十九届长三角植物科学学术研讨会	2022.10.28
16	巩志忠	ABA signaling and plant drought stress	植物逆境适应机制国际学术研讨会	2022.11.17
17	杨淑华	Molecular mechanisms of cold tolerance in *Arabidopsis* and maize	The 9th international horticulture research conference	2022.11.20
18	徐明良	Maize ZmWAKL-mediated immunity in quantitative resistance to gray leaf spot	7th international symposium on genomics and crop genetic improvement - genomic breeding	2022.11.29

序号	报告人	报告题目	会议名称	会议时间
19	王向锋	植物微管结合蛋白响应环境信号调控微管骨架的机制研究	全国电子显微学学术年会	2022.11.25

植物生理学与生物化学国家重点实验室

State Key Laboratory of Plant Physiology and Biochemistry

http://sklppb.cau.edu.cn/

（三）在国内外讲学

序号	姓名	报告题目	讲学单位	讲学日期
1	秦　峰	Genetic determinants of drought response and tolerance in maize	中国农科院作物研究所	2022.03.15
2	杨小红	殊途同归：揭示玉米和水稻趋同选择的奥秘	中国科学院遗传与发育生物学研究所	2022.03.28
3	杨小红	殊途同归：揭示玉米和水稻趋同选择的奥秘	中国农科院作科所	2022.04.01
4	杨小红	殊途同归：玉米和水稻趋同选择的奥秘	中国农业大学	2022.04.06
5	杨小红	殊途同归：揭示玉米和水稻趋同选择的奥秘	北京市农林科学院玉米研究所	2022.04.07
6	杨淑华	植物感受和应答低温信号的分子机制	清华大学	2022.04.13
7	杨小红	Convergent selection of a wd40 protein that enhances grain yield in maize and rice	aBIOTECH Virtual Seminar	2022.04.15
8	杨小红	Convergent selection of a wd40 protein that enhances grain yield in maize and rice	先正达生物科技有限公司	2022.04.19
9	杨小红	Convergent selection of a wd40 protein that enhances grain yield in maize and rice	长江大学	2022.04.22
10	周文焜	植物根系发育与根干细胞调控分子机理	北京林业大学	2022.04.22
11	秦　峰	Genetic dissection of drought response and resistance in maize	中国科学院分子植物卓越创新中心	2022.04.23
12	杨淑华	植物耐寒性的分子调控机制	南京农业大学	2022.04.26
13	杨淑华	植物响应低温胁迫的分子机制	山西大学	2022.04.27
14	徐明良	玉米 Helitron 转座子诱导的粗缩病隐性数量抗性研究	中国科学与技术大学	2022.05.07
15	王　毅	植物感受低钾胁迫信号的机制	中国科技大学	2022.05.07
16	杨小红	殊途同归：玉米和水稻趋同选择的遗传规律	南京大学	2022.05.13
17	杨小红	殊途同归：玉米和水稻趋同选择的遗传规律	济南大学	2022.05.16
18	杨小红	殊途同归：玉米和水稻趋同选择的遗传规律	河南大学	2022.05.19
19	杨淑华	植物感受和应答低温信号的分子机制	上海师范大学	2022.05.24
20	杨淑华	植物感知和应答低温信号	上海分子植物科学卓越创新中心	2022.05.31
21	秦　峰	玉米抗旱性的遗传解析及基因克隆	Cell Press Live	2022.06.29
22	郑绍建	抗营养逆境之策略	中国科学院南京土壤研究所	2022.06.29
23	徐明良	玉米抗病分子育种现状与趋势	扬州大学	2022.08.01
24	杨小红	殊途同归：玉米和水稻趋同选择的遗传规律	科学咖啡沙龙	2022.08.25

序号	姓名	报告题目	讲学单位	讲学日期
25	徐　凌	Sorghum root microbiome under drought stress	北京农林科学院	2022.08.26
26	徐明良	玉米抗病分子育种现状与趋势	内蒙古农业大学	2022.09.10
27	秦　峰	玉米抗旱基因 *ZmSRO1d-R* 激活 ZmRBOHC 调控抗旱性与产量的平衡	第四届国际三角洲暨盐碱地种业创新高峰论坛	2022.09.24
28	田　丰	玉米驯化与适应的分子遗传基础	广州大学	2022.09.30
29	杨淑华	植物耐冷性的分子调控机制	2022 作物设计 Crop Design 线上系列研讨会	2022.10.08
30	田　丰	玉米驯化与适应的分子遗传基础	华南农业大学	2022.10.10
31	李继刚	Light signal transduction in plants	首都师范大学	2022.10.13
32	宋任涛	玉米储藏蛋白合成与胚乳发育研究	浙江大学现代种业研究所	2022.10.13
33	杨淑华	植物感知和应答低温信号的分子机制	广州大学	2022.10.22
34	秦　峰	玉米抗旱性的遗传解析及基因克隆	浙江大学	2022.10.27
35	傅　缨	调控植物细胞极性生长的 ROP GTPases 信号网络	北京师范大学	2022.10.28
36	田　丰	玉米驯化与适应的分子遗传基础	中国科学院西双版纳热带植物园	2022.11.05
37	徐　凌	Sorghum root microbiome under drought stress	西北农林科技大学	2022.11.07
38	田　丰	玉米驯化与适应的分子遗传基础	山西农业大学	2022.11.11
39	郑绍建	STOP1 与植物营养逆境响应	上海师范大学	2022.11.15
40	徐　娟	MAPK 级联信号调控植物生长发育	南方科技大学	2022.11.17
41	徐　娟	MAPK 级联信号调控植物生长发育	兰州大学	2022.11.22
42	田晓莉	棉花全程机械化栽培关键化控技术	河北省农林科学院棉花研究所	2022.11.24
43	李继刚	Light signal transduction in plants	广州大学（在线报告）	2022.11.07
44	徐　凌	Sorghum root microbiome under drought stress	南方科技大学	2022.12.01
45	杨淑华	Molecular mechanism of plant response to cold stress	北京大学	2022.12.02
46	齐俊生	VDAL 在植物胞内的作用机理研究	山东农业大学	2022.12.28

九、学术组织任职

序号	姓名	学术组织名称	职务
1	杨淑华	九三学社第十四届中央委员会教育文化专门委员会	副主任
2	杨淑华	中国农业大学女教授协会	会长
3	杨淑华	中国植物学会第十六届理事会	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	理事
5	杨淑华	F1000Prime	1000 Faculty Member in Plant Biology（Plant-Environment Interactions Section）
6	傅　缨	北京细胞生物学会	理事
7	傅　缨	中国细胞生物学学会细胞结构与功能分会	委员
8	傅　缨	中国遗传学会发育遗传专业委员会	委员
9	李召虎	中国农学会棉花分会	副理事长
10	李召虎	中国作物学会	监事长
11	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
12	孙传清	中国作物学会分子育种分会	理事
13	孙传清	中国农学会遗传资源分会	常务理事
14	金危危	中国作物学会	副理事长
15	金危危	中国种子协会	副会长
16	金危危	中国作物学会人才培养与教育专业委员会	会长
17	金危危	中国作物学会	副理事长
18	任东涛	北京生物化学与分子生物学会	常务理事
19	田晓莉	中国农学会棉花分会第十届理事会	理事
20	田晓莉	中国作物学会棉花专业委员第一届理事会	委员
21	赖锦盛	中国作物学会	第十一届理事会副秘书长
22	赖锦盛	中国作物学会	分子育种专业委员会副会长
23	赖锦盛	中国农业生物技术学会	第六届理事会理事
24	王　毅	中国生物物理学会膜生物学分会	理事
25	王　毅	中国植物学会细胞生物学专业委员会	委员
26	王　毅	中国遗传学会青年委员会	委员
27	李继刚	中国植物学会植物生理及分子生物学专业委员会	委员
28	李继刚	中国细胞生物学学会植物器官发生分会	委员
29	李继刚	中国植物生理与植物分子生物学学青年工作委员会	委员
30	王喜庆	中国农业生物技术学会植物表型组学分会学术委员会	主任
31	王喜庆	中国生物物理学会表型组学分会委员	委员
32	王喜庆	全国植物新品种测试标准化技术委员会	委员
33	齐俊生	中国植保学会	专业委员
34	郑绍建	中国植物生理与植物分子生物学学会	常务理事
35	郑绍建	浙江省植物生理与植物分子生物学学会	理事长
36	寿惠霞	浙江省植物生理与植物分子生物学学会	副会长
37	刘建祥	浙江省植物生理与植物分子生物学学会	秘书长

序号	姓名	学术组织名称	职务
38	金崇伟	浙江省土壤肥料学会	常务理事
39	金崇伟	中国植物生理与植物分子生物学学会	理事
40	金崇伟	中国植物营养与肥料学会	植物营养生物学专业委员会委员
41	田　丰	中国作物学会第二届分子育种专业委员	副秘书长
42	田　丰	中国作物学会玉米专业委员会	委员
43	田　丰	中国遗传学学会数量遗传学分会	委员
44	徐明良	中国作物学会玉米专业委员会	秘书长
45	徐纪明	浙江省植物生理与植物分子生物学学会	副秘书长
46	李　溱	中国化学会农业化学专业委员会	理事
47	李　溱	中国质谱学会	理事
48	李　溱	中国生物化学与分子生物学会蛋白质组学专业委员会植物蛋白质中学工作组	理事
49	陈其军	中国遗传学会基因组编辑分会	委员

十、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	Journal of Integrative Plant Biology	Editor
4	杨淑华	Journal of Plant Physiology	Senior Editor
5	杨淑华	Stress Biology	Editor
6	杨淑华	植物学报	副主编
7	郭　岩	Journal of Genetics and Genomics	编委
8	郭　岩	Plant and Cell Physiology	编委
9	巩志忠	Plant Physiology	编委
10	巩志忠	Journal of Integrative Plant Biology	主编
11	王　毅	Journal of Integrative Plant Biology	编委
12	王　毅	New Phytologist	顾问编委
13	傅　缨	New Phytologist	顾问编委
14	傅　缨	植物学报	编委
15	傅　缨	植物生理学报	编委
16	秦　峰	Plant Journal	Editor
17	秦　峰	Plant Molecular Biology	Associate Editor
18	秦　峰	Molecular Breeding	Associate Editor
19	秦　峰	植物学报	编委
20	秦　峰	Trends in Plant Science	Advisory Board
21	苏　震	Frontiers in Genetics	副编辑
22	苏　震	Scientific Reports	编委
23	任东涛	植物学报	编辑
24	孙传清	作物学报	副主编
25	孙传清	Crop Journal	编委
26	赖锦盛	Journal of Integrative Plant Biology	编委
27	赖锦盛	Plant Cell	编委
28	金危危	Chromosome Research	编委
29	金危危	Crop Journal	编委
30	金危危	作物学报	副主编
31	金危危	中国农业大学学报	副主任委员
32	徐明良	作物学报	副主编
33	徐明良	玉米科学	编委
34	徐明良	Theoretical and Applied Genetics	编委
35	徐明良	Crop Journal	编委
36	徐明良	Frontiers in Plant Science	编委
37	徐明良	Molecular Breeding	编委
38	宋任涛	遗传	编委
39	宋任涛	玉米科学	编委
40	田　丰	Journal of Plant Biology	编委
41	田　丰	Molecular Breeding	编委
42	田　丰	作物学报	编委
43	田晓莉	棉花学报	编委
44	田晓莉	作物学报	编委

序号	人员姓名	期刊名称	职务
45	田晓莉	Journal of Cotton Research	编委
46	毛同林	植物学报	编委
47	周文焜	Molecular Plant	Feature Editor
48	李继刚	Journal of Integrative Plant Biology	Editor
49	李继刚	Stress Biology	Editor
50	李继刚	Frontiers in Plant Science	Guest Associate Editor
51	王良省	International Journal of Molecular Medicine	Guest Editor
52	王良省	Frontiers in Plant Science	Review Editor
53	郑绍建	Annals of Botany	地区编委
54	郑绍建	Journal of Integrative Plant Biology	编委
55	寿惠霞	Frontiers in Plant Sciences	编辑
56	寿惠霞	Plants	编辑
57	寿惠霞	植物生理学报	编辑
58	寿惠霞	大豆科学	编辑
59	寿惠霞	浙江农业学报	编辑
60	刘建祥	BMC Plant Biology	副编辑
61	刘建祥	aBIOTECH	编委
62	刘建祥	Stress Biology	编委
63	王智烨	Frontiers in Plant Science	Guest Associate Editor
64	金崇伟	浙江大学学报（农业与生命科学版）	编委
65	杨永青	西北植物学报	编委
66	刘凤霞	Plants	编委

十一、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	植物分子生物学	植物响应低温胁迫的分子机制
2	杨淑华	曾　榕	植物分子生物学	玉米耐低温胁迫的分子机制
3	郭　岩	马　亮	植物分子生物学	植物耐盐分子调控机制
4	郭　岩	李建芳	植物分子生物学	拟南芥盐胁迫信号传导与适应的调控与生理机制
5	郭　岩	刘国永	植物分子生物学	植物囊泡运输与耐盐机制
6	郭　岩	张天任	植物分子生物学	植物微丝骨架动态与耐盐机制
7	巩志忠	马爱芳	玉米抗旱	玉米抗旱
8	傅　缨	石　磊	发育生物学	早期花药发育的调控机制研究
9	毛同林	王晓红	植物细胞骨架	中国博士后科学基金面上资助
10	毛同林	邓　佳	植物细胞骨架	植物生长发育可塑性机制
11	李继刚	韩　润	植物抗逆机理	避荫反应机制
12	李继刚	齐立娟	植物抗逆机理	避荫反应机制
13	李继刚	彭　晶	植物抗逆机理	植物光信号转导
14	蒋才富	张　鸣	玉米抗盐机制	玉米抗盐机制
15	蒋才富	梁晓燕	植物逆境	玉米抗盐基因的挖掘利用
16	蒋才富	周雪雁	玉米耐盐碱的分子机制	玉米耐盐碱的分子机制
17	蒋才富	尹　攀	玉米耐盐碱的分子机制	玉米耐盐碱的分子机制
18	王喜庆	刘敏国	植物形状和结构分析	玉米表型组分析技术
19	张　静	王亚璐	植物分子生物学	低氮调控植物根可塑性生长的分子机制
20	孙传清	聂　静	作物果实发育分子机制	水稻籽粒发育机制
21	赖锦盛	李　元	玉米遗传育种	玉米单倍体育种
22	赖锦盛	刘胜男	玉米遗传育种	作物基因编辑器的递送体系建立
23	赖锦盛	张莉莉	玉米遗传育种	单倍体育种
24	赖锦盛	李卓洋	玉米遗传育种	玉米基因编辑技术
25	赖锦盛	徐　峰	玉米遗传育种	蛋白-核酸互作界面识别和工具的开发
26	赖锦盛	李建锐	玉米籽粒发育	玉米籽粒发育机制
27	赖锦盛	张美玲	作物遗传育种	玉米氮素利用的分子机制
28	赖锦盛	申晓蒙	玉米遗传育种与发育生物学	玉米雌穗高密度转录组研究
29	徐明良	钟　涛	玉米抗病基因挖掘与抗性机制阐释	玉米灰斑病抗病基因克隆及其抗病机理
30	徐明良	朱　芒	玉米抗病基因挖掘与抗性机制阐释	玉米灰斑病抗病基因克隆及其抗病机理
31	徐明良	邓穗宁	玉米抗病基因挖掘与抗性机制阐释	玉米粗缩病抗病基因克隆及其抗病机理
32	徐明良	张倩倩	抗病机理	丝黑穗抗病机理
33	徐　凌	徐海燕	玉米微生物组	玉米抗茎腐病微生物组
34	宋任涛	王　群	玉米籽粒发育调控	玉米籽粒发育调控
35	田　丰	郭　丽	玉米功能基因组	玉米花期基因克隆与功能分析
36	田　丰	王成龙	玉米功能基因组	玉米叶夹角基因克隆与功能分析
37	田　丰	梁亚盟	玉米功能基因组	玉米花期 QTL 的克隆
38	田　丰	任如昌	玉米驯化	玉米花期 QTL 的克隆

序号	导师	姓名	研究方向	在实验室承担的课题
39	杨小红	陈文康	玉米基因组学	玉米/水稻穗粒数基因的聚合选择
40	杨小红	张人予	玉米主要产量性状的遗传基础	*EL3* 基因的分子机理研究
41	杨小红	张　璇	玉米主要产量性状的遗传基础	玉米穗行数基因克隆及功能解析
42	寿惠霞	李钦雪	植物生理学	水稻功能基因组学研究
43	毛传澡	郭润泽	植物生理学	水稻功能基因组学研究
44	刘建祥	王梅敬	作物抗逆机制	植物热胁迫响应机制
45	刘建祥	李劲宇	作物抗逆机制	植物热胁迫响应机制
46	刘建祥	尚　菲	水稻温敏雄性不育	水稻温敏雄性不育
47	毛传澡	朱建树	根构型	水稻根构型
48	毛传澡	李　勇	根构型	水稻根构型
49	毛传澡	王　飞	磷信号调控	水稻磷信号调控
50	毛传澡	任美燕	根构型	水稻根构型
51	王智烨	乔露露	养分高效利用	染色质重塑蛋白在植物缺营养胁迫响应机制研究
52	王智烨	李兵杰	养分高效利用	RNA 代谢在植物缺营养胁迫响应机制研究
53	王智烨	董伟国	养分高效利用	RNA 介导的植物缺营养胁迫响应机制研究
54	徐　娟	张　严	植物信号转导	植物生长发育的信号调控网络
55	徐　娟	邵伊明	植物信号转导	植物生长发育的信号调控网络
56	秦　峰	杨世平	玉米基因组学	玉米基因组比较分析
57	秦　峰	田　甜	功能基因组学	玉米抗旱自交系基因组结构变异解析
58	秦　峰	赵　军	玉米抗旱	玉米开花期抗旱性的遗传解析
59	秦　峰	王妍妍	玉米抗旱	玉米根系调控抗旱性的遗传解析
60	王良省	赵　欢	植物活性氧信号转导	植物单线态氧信号转导的分子机理

十二、开放课题

课题编号	题目	负责人	职称	单位	合作教授
SKLPPBKF2103	玉米萌发期响应渗透胁迫的遗传基础解析	李　丛	讲师	沈阳农业大学	田　丰
SKLPPBKF2105	玉米花粉特异 *CRISPR/Cas9* 基因编辑遗传转化体系的构建	祁巍巍	副教授	上海大学	宋任涛
SKLPPBKF2107	番茄激酶 OST1 调控开花和干旱应答的机制研究	祝英方	教授	河南大学	李继刚
SKLPPBKF2109	玉米穗腐病抗性主效 QTL-*qRger7.1* 的精细定位	张　艳	副研究员	吉林省农业科学院	徐明良
SKLPPBKF2110	昌 7-2 耐盐性改良材料在吉林省白城市盐碱地的表型分析	宋新元	副研究员	吉林省农业科学院	蒋才富
SKLPPBKF2112	*ZmSUS4* 调控玉米耐旱性的机制研究	王宏伟	副教授	长江大学	秦　峰
SKLPPBKF2113	玉米温敏无雄穗基因 *Tvt2* 的克隆及功能分析	谢仕意	博士后	湖南农业大学	金危危
SKLPPBKF2114	白菜组蛋白 HIS4 参与花期和环境互作调控的分子机制	苏同兵	副研究员	北京市农林科学院蔬菜研究中心	任东涛
SKLPPBKF2115	搭建优化的基因编辑平台实现广西普通野生稻的从头驯化	张　强	助研	江苏省农业科学院粮食作物研究所	陈其军
SKLPPBKF2116	拟南芥微丝解聚因子 ADF1 在盐胁迫中的作用机制研究	王显玲	副教授	沈阳农业大学	毛同林
SKLPPBKF2117	植物激素对重金属 Cd 胁迫龙须菜生长的缓解作用机制	陈晓娇	助研	宁波大学	段留生
SKLPPBKF2118	链格孢菌诱导植物病害过程中的单线态氧信号与水杨酸信号交叉对话机制	陈世国	教授	南京农业大学	王良省

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。

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、拟南芥钾离子通道AKT1活性调节的结构基础解析

钾离子是植物生长发育所必需的矿物质营养元素，在植物细胞的基本生命过程以及植物响应逆境胁迫中发挥重要作用。拟南芥钾离子通道AKT1是介导根细胞从土壤中吸收钾离子的重要蛋白，其活性受到严格调控。AKT1可以形成同源四聚体通道，在静息状态下活性很低，受到逆境胁迫后，可以被钙结合蛋白CBL1/9和丝氨酸/苏氨酸蛋白激酶CIPK23信号通路磷酸化激活。同时，钾离子通道调节亚基KC1可以与AKT1形成异源四聚体通道从而调控AKT1的活性。然而，AKT1通道被激活打开以及活性调节的机制尚不明确。我们利用冷冻电镜技术解析了钾离子通道AKT1处于静息和磷酸化激活两种状态的蛋白三维结构，以及AKT1组成型活性突变体和AKT1/KC1复合体的结构。发现磷酸化的AKT1会使其C-linker结构域发生构象变化，从而自静息状态下的二重对称结构转变为激活状态下的四重对称结构。据此认为AKT1存在这种特有的对称性转换，即低活性状态下AKT1在胞质一侧呈现二重对称结构，而在高活性状态下，胞内区由二重对称转变为四重对称结构。KC1与AKT1形成胞内区为二重对称的异源四聚体。本研究揭示了AKT1处于不同活性状态下的构象差异、以及不同构象之间转换的分子机制，该结果为提高植物的钾离子利用效率提供重要理论基础，也为靶向调节AKT1活性进行分子育种提供了科学依据。该研究成果于2022年9月发表在*Nature Commun*（Lu et al., 2022）。

Structural Basis for the Activity Regulation of a Potassium Channel AKT1 from *Arabidopsis*

The voltage-gated potassium channel AKT1 is responsible for primary K^+ uptake in *Arabidopsis* roots. AKT1 is functionally activated through phosphorylation and negatively regulated by a potassium channel α-subunit KC1. However, the molecular basis for the modulation

mechanism remains unclear. Here we report the structures of AKT1, phosphorylated-AKT1, a constitutively-active variant, and AKT1-KC1 complex. AKT1 is assembled in 2-fold symmetry at the cytoplasmic domain. Such organization appears to sterically hinder the reorientation of C-linkers during ion permeation. Phosphorylated-AKT1 adopts an additional 4-fold symmetric conformation at cytoplasmic domain, which indicates conformational changes associated with symmetry switch during channel activation. To corroborate this finding, we performed structure-guided mutagenesis to disrupt the dimeric interface and identified a constitutively-active variant Asp379Ala mediates K^+ permeation independently of phosphorylation. This variant predominantly adopts a 4-fold symmetric conformation. Furthermore, the AKT1-KC1 complex assembles in 2-fold symmetry. Together, our work reveals structural insight into regulatory mechanism for AKT1 (Lu et al., *Nat Commun*, 2022).

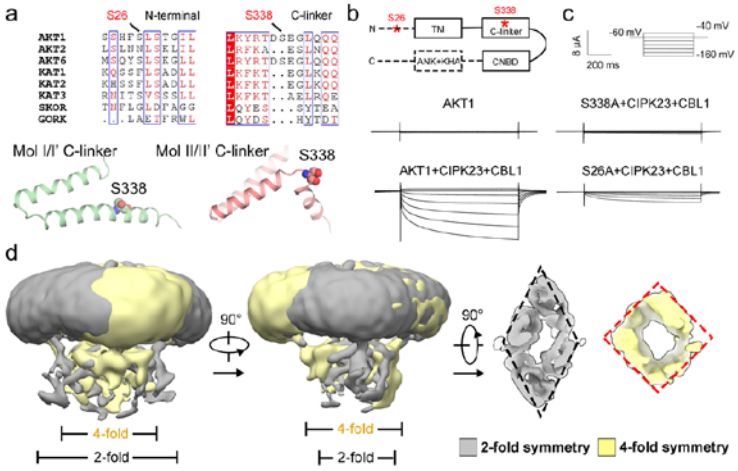


图1、AKT1静息状态与激活状态的结构转换示意图。

Figure 1. Functional validation and structural determination of the potassium channel AKT1 from *Arabidopsis*.

2、类受体蛋白激酶BAK1调控植物钾吸收的分子机制解析

钾是植物生长发育所必需的大量矿质元素之一。土壤中可供植物吸收利用的自由钾离子浓度通常较低，植物经常遭受低钾胁迫。目前，有关植物如何感受低钾胁迫的分子机制还知之甚少。已有的研究表明类受体蛋白激酶（Receptor-like protein kinase, RLK）在植物感受环境信号及逆境胁迫过程中发挥了重要作用。本研究发现拟南芥类受体蛋白激酶BAK1（Brassinosteroid insensitive 1-Associated Kinase 1）参与低钾胁迫的感受和应答过程。在低钾培养基上，*bak1*突变体表现出冠部叶片发黄，生长受抑制的表型。*bak1*突变体的钾离子吸收能力显著低于野生型，说明BAK1参与调控拟南芥根部的钾离子吸收过程，并且不依赖于BR（Brassinosteroid）信号通路和免疫信号通路。研究发现BAK1与根细胞质膜上的H^+-ATPase AHA2（*Arabidopsis* H^+-ATPase isoform 2）存在直接的蛋白互作，并且BAK1能够磷酸化AHA2的C端，从而增强AHA2的质子泵活性，进而促进根部钾离子吸收过程。该研究结果表明，类受体蛋白激酶BAK1和AHA2共同参与低钾胁迫的感受和应答过程。低钾条件下，BAK1通过磷酸化AHA2从而增强其活性，在根细胞建立跨细胞质膜的质子电化学势梯

度，进而促进钾通道AKT1和钾转运体HAK5所介导的根部钾离子吸收，以此来应对低钾胁迫。该研究结果为深入解析植物响应低钾胁迫的分子调控机制提供了重要实验证据，也进一步完善了植物钾吸收的分子调控网络。该研究成果于2022年8月发表在*Plant Physiol*（Wang et al., 2022）。

Receptor-like Protein Kinase BAK1 Promotes Potassium Uptake by Phosphorylating H⁺-ATPase AHA2 under Low Potassium Stress

Potassium (K^+) is one of the essential macronutrients for plant growth and development. However, the available K^+ concentration in soil is relatively low. Plant roots can perceive low K^+ (LK) stress, then enhance high-affinity K^+ uptake by activating H^+-ATPases in root cells, but the mechanisms are still unclear. Here, we identified the receptor-like protein kinase Brassinosteroid Insensitive 1-Associated Receptor Kinase 1 (BAK1) that is involved in LK response by regulating the *Arabidopsis* plasma membrane H^+-ATPase isoform 2 (AHA2). The *bak1* mutant showed leaf chlorosis phenotype and reduced K^+ content under LK conditions, which was due to the decline of K^+ uptake capacity. BAK1 could directly interact with the AHA2 C terminus and phosphorylate T858 and T881, by which the H^+ pump activity of AHA2 was enhanced. The constitutively activated form $AHA2^{\Delta 98}$ and phosphorylation-mimic form $AHA2^{T858D}$ or $AHA2^{T881D}$ could complement the LK sensitive phenotypes of both *aha2* and *bak1* mutants. Together, our data demonstrate that BAK1 phosphorylates AHA2 and enhances its activity, which subsequently promotes K^+ uptake under LK conditions (Wang et al., *Plant Physiol*, 2022).

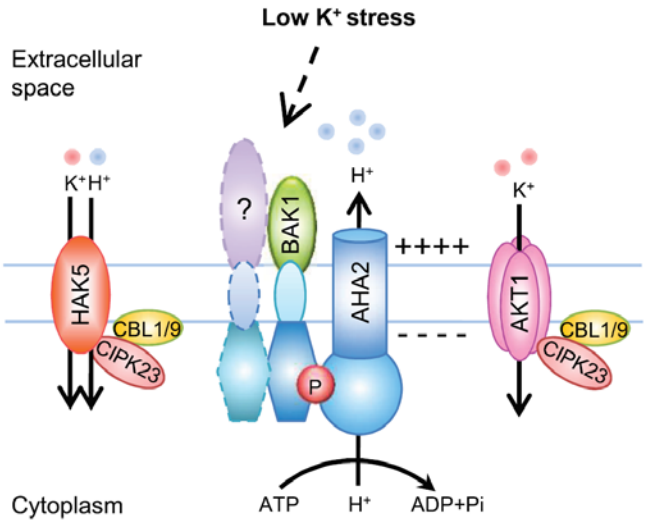


图2、BAK1响应低钾胁迫调控AHA2活性促进根部钾吸收的工作模型。

Figure 2. Working model of AHA2 phosphorylation regulation by BAK1 in *Arabidopsis* response to LK stress.

（二） 研究成果

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

1. Lu Y#, Yu M#, Jia Y#, Yang F, Zhang Y, Xu X, Li X, Yang F, Lei J, **Wang Y***, Yang G* (2022)

Structural basis for the activity regulation of a potassium channel AKT1 from *Arabidopsis*. ***Nat Commun*** 13: 5682.

2. Wang ZF, Xie ZM, Tan YL, Li JY, Wang FL, Pei D, Li Z, Guo Y, Gong ZZ, **Wang Y*** (2022) Receptor-like protein kinase BAK1 promotes potassium uptake by phosphorylating H^+-ATPase AHA2 under low potassium stress. ***Plant Physiol*** 189: 2227-2243.
3. Wang ZF#, Mi TW#, Gao YQ, Feng HQ, **Wu WH**, **Wang Y*** (2022) STOP1 regulates *LKS1* transcription and coordinates K^+/NH_4^+ balance in *Arabidopsis* response to low-K^+ stress. ***Int J Mol Sci*** 23: 383.
4. Sun MM, Tian Y, Chun M, **Chen YF*** (2022) The ubiquitin E3 ligase PRU2 modulates phosphate uptake in *Arabidopsis*. ***Int J Mol Sci*** 23: 2273.

专利授权：

1. 蛋白 PNR1 在培育磷营养高效植物品种中的应用。申请人：**陈益芳**，**武维华**，王雪；专利号：ZL201910422464.4；授权日期：2022 年 11 月 01 日。
2. ZmbHLH148 蛋白及其编码基因在调控植物抗旱性中的应用。申请人：**陈丽梅**，**武维华**，王瑞芳，**李希东**，郝杰，王喜庆；专利号：ZL202010143364.0；授权日期：2022 年 11 月 22 日。

（三） 研究队伍

固定人员：

武维华（课题组长），陈益芳，陈丽梅，王毅，汪洋，李希东。

研究生：

王红阳，孙咪咪，刘梦媛，姬赟，韩武，王海峰，田燕，李小梅，王少帅，敬思，谈亚兰，郝杰，布热比艳木·吾布力卡斯木，刘瑾洁，春梅，李瑞祥，陈卓，胡英迎，谭佩佩，郑璐颖，谢仲梅，智晓娜，李营营，鲍萍，贾冬云，汪昕珑，李佳颖，吴子麒，孙伟娜，岳林迪，贾艳聪，崔亚楠，张曼，郭慧玲，田梦芝，戚留冉，黄逸之，王康祺，秦毅州，路学瑶，张涵，日贤，吴逸航，贾晶晶，胡楚恩，廖佳慧。

杨淑华课题组

杨淑华，教授。

研究方向：植物感受与响应低温胁的分子机制，低温信号和光信号互作机制。

（一） 研究进展

1、mGWAS 揭示 *ZmICE1* 自然变异调控玉米耐冷性的分子机制

作为重要的非生物胁迫，低温胁迫对农作物产量品质有严重的影响。玉米是重要农作物，起源于热带地区，对低温环境非常敏感。研究玉米响应低温的分子机制，挖掘优良等位变异，对提高作物耐冷性，保障国家粮食安全具有重要意义。目前人们对玉米低温响应的分子机制研究尚处于起步阶段，可利用的优势基因资源仍有待进一步发掘。该研究使用高分辨质谱对 245 份自交系材料进行常温及低温处理下的非靶标代谢组学分析，结合 mGWAS 分析，发现转录因子 ZmICE1 参与低温诱导的代谢调控过程。过量表达 *ZmICE1* 可显著增强玉米萌发期及苗期耐冷性，表明 ZmICE1 是玉米耐冷性的正调控因子。利用 RNA-seq 及 ChIP-seq 共鉴定了 802 个 ZmICE1 直接调控的冷响应靶基因。有趣的是，除 *ZmDREB1s*、*ZmERFs* 等冷响应基因外，超过半数靶基因参与各种代谢过程。其中一类 *ZmASs*（*ASPARAGINE SYNTHETASES*）基因编码 Glu-Asn 合成关键酶，在氮代谢中发挥重要作用。候选基因关联分析发现 *ZmICE1* 启动子区 SNP-465 是影响 *ZmICE1* 基因表达的重要位点，该位点变异影响 ZmMYB39 转录因子与 *ZmICE1* 启动子的结合，从而影响 *ZmICE1* 转录水平。在耐冷单倍型中，ZmMYB39 与 *ZmICE1* 启动子区的结合能力增强，*ZmICE1* 转录水平增加，ZmICE1 蛋白积累，一方面促进冷响应基因如 *DREB1s* 的表达；另一方面抑制 *ZmAS* 的表达减少 Glu/Asn 的生物合成，从而缓解由 Glu 引起的线粒体活性氧 mtROS 的产生，进而解除 mtROS 对 *DREB1s* 表达的抑制。该研究结果为阐明玉米响应低温分子机制提供重要理论依据，为作物性状改良提供新的思路，展示了基于高分辨质谱的代谢组学技术在解析玉米抗逆性方面的应用潜力（Jiang et al., *Nat Plants*, 2022）。

Natural Polymorphism of *ZmICE1* Contributes to Amino Acid Metabolism That Impacts Cold Tolerance in Maize

Cold stress negatively affects maize (*Zea mays* L.) growth, development, and yield. Metabolic adjustments contribute to the adaption of maize under cold stress. We show here that the transcription factor INDUCER OF CBF EXPRESSION 1 (ZmICE1) plays a prominent role in

reprogramming metabolome and maintaining amino acid homeostasis during cold stress in maize. Derivatives of amino acids glutamate/asparagine (Glu/Asn) induce a burst of mitochondrial reactive oxygen species, which suppress the cold-mediated induction of *DEHYDRATION RESPONSE ELEMENT-BINDING PROTEIN 1* (*ZmDREB1*) genes and impair cold tolerance. ZmICE1 blocks this negative regulation of cold tolerance by directly repressing the expression of *Asn synthetase* genes, which function in Glu biosynthesis. Natural variation at the *ZmICE1* promoter determines the binding affinity of the transcriptional activator ZmMYB39, a positive regulator of cold tolerance in maize, resulting in different degrees of *ZmICE1* transcription and cold tolerance across inbred lines. Our study thus unravels a mechanism of cold tolerance in maize and provides potential targets for engineering cold-tolerant varieties (Jiang et al., *Nat Plants*, 2022).

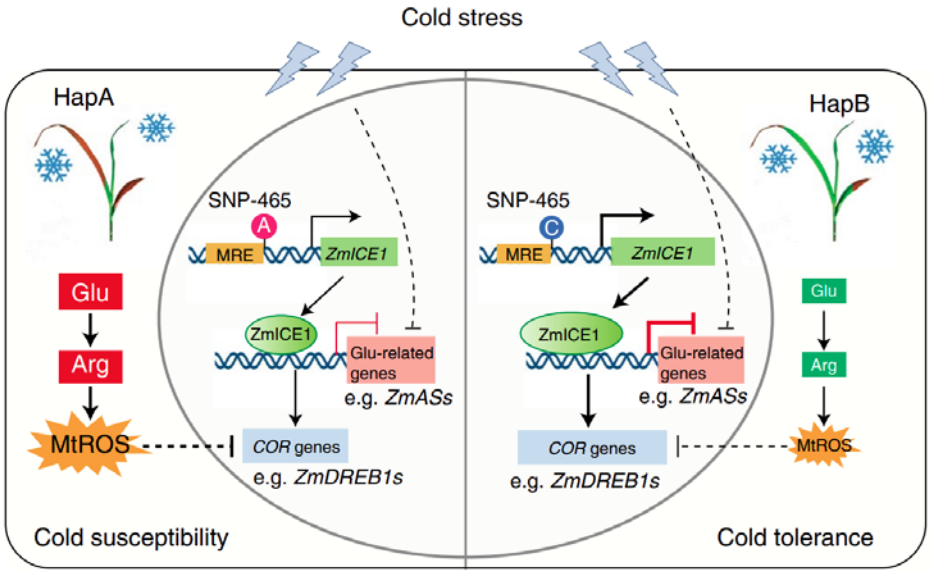


图1、转录因子ZmICE1介导氨基酸代谢和玉米耐冷性的分子模型。

Figure 1. Proposed model of ZmICE1-mediated amino acid metabolism and cold tolerance in maize.

2、玉米 bZIP68 转录因子调控玉米耐冷性的分子机制

该研究通过对 700 多份玉米过表达株系进行苗期低温表型的筛选，鉴定了一个负调控玉米耐冷性的基因 *bZIP68*。bZIP68 与玉米耐低温负调控因子 MPK8 在细胞核中互作，被其磷酸化从而促进 bZIP68 在低温下的积累。同时，MPK8 所介导的磷酸化修饰增强 bZIP68 对下游靶基因 *DREB1* 启动子的结合，负调控 *DREB1* 等冷响应基因的表达。值得一提的是 *bZIP68* 的突变提高玉米耐冷性，同时对产量相关性状并没有明显影响。玉米在经历漫长的驯化过程中受自然选择与人类选择的影响导致其核苷酸多样性显著下降。之前的研究表明 *bZIP68* 基因组区域在玉米早期驯化过程中被选择。我们通过重测序比对发现，*bZIP68* 在玉米基因组中的启动子区域与祖先种大刍草（*Z. mays* ssp. *parviglumis*、*Z. mays* ssp. *Mexicana*）比较具有很大的差异，其中玉米 *bZIP68* 具有一个位于-972（B73）位点的 358-bp 的片段插入。该片段的插入使 *bZIP68* 在玉米中的表达量升高，耐冷性下降。

该结果显示在玉米驯化过程中 *bZIP68* 的耐冷优势等位变异并没有被利用，*bZIP68* 在大刍草中的耐冷优势等位变异有可能作为培育耐冷玉米品种的重要靶点，这为耐冷玉米新品种培育提供新的基因资源（Li et al., *Plant Cell*, 2022），*Plant Cell* 杂志同期发表“Out in the cold: variation in the *ZmbZIP68* promoter modulates cold tolerance in maize”专评，重点介绍了该项成果的研究意义。

The Transcription Factor bZIP68 Negatively Regulates Cold Tolerance in Maize

Maize (*Zea mays*) originated in tropical areas and is thus susceptible to low temperatures, which pose a major threat to maize production. Our understanding of the molecular basis of cold tolerance in maize is limited. Here, we identified bZIP68, a basic leucine zipper (bZIP) transcription factor, as a negative regulator of cold tolerance in maize. Transcriptome analysis revealed that bZIP68 represses the cold-induced expression of *DREB1* transcription factor genes. The stability and transcriptional activity of bZIP68 are controlled by its phosphorylation at the conserved Ser250 residue under cold stress. Furthermore, we demonstrated that the *bZIP68* locus was a target of selection during early domestication. A 358-bp insertion/deletion (Indel-972) polymorphism in the *bZIP68* promoter has a significant effect on the differential expression of bZIP68 between maize and its wild ancestor teosinte. This study thus uncovers an evolutionary cis-regulatory variant that could be used to improve cold tolerance in maize (Li et al., *Plant Cell*, 2022).

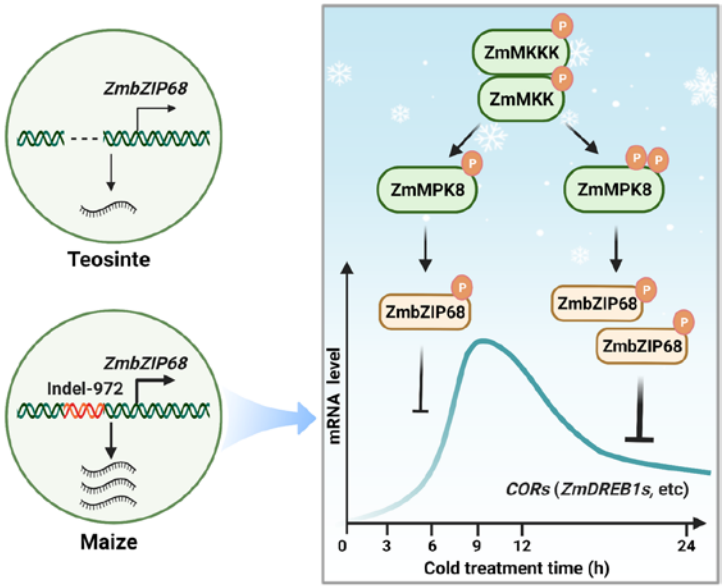


图2、MPK8-bZIP68模块调控玉米耐冷性的分子模型。

Figure 2. Model of the role of bZIP68 in regulating the cold response in maize.

3、CPK28-NLP7 介导低温诱导的特异钙信号的感知与解码机制

钙离子（Ca^{2+}）作为重要的次级信号分子参与植物的生长发育及环境信号的应答。低温诱导的细胞膜固化可能被定位于细胞膜上的蛋白等感知，进而迅速诱导细胞质中 Ca^{2+}浓度增加，产生特异

的 Ca^{2+}信号（Ca^{2+} signature）。很早之前的研究就表明低温特异 Ca^{2+}信号是低温应答基因表达的重要调控因子。然而，植物是如何感知并解码低温诱导的特异 Ca^{2+}信号尚不清楚。植物中主要含有三类钙离子感知蛋白，包括钙调素蛋白（CaM）、钙调神经磷酸酶 B 样蛋白（CBL）和钙离子依赖型蛋白激酶（CPK）。其中，CPK 蛋白既能结合钙离子又能通过其激酶域直接传递 Ca^{2+}信号，因此我们分析 CPK 家族成员在低温下的基因表达和激酶活性，发现 *CPK28* 基因受低温显著诱导表达，CPK28 激酶活性被低温迅速诱导激活，该过程依赖于低温诱导的 Ca^{2+}信号；CPK28 的 Ca^{2+}结合活性和激酶活性是其正调控植物低温应答所必需的。质谱分析发现细胞质/细胞核定位的转录因子 NLP7 可能和 CPK28 存在于同一个蛋白复合体中，通过 pull-down 实验、免疫共沉淀实验验证两者存在相互作用，双分子荧光互补实验表明两者在细胞膜附近互作。进一步研究发现 CPK28 磷酸化 NLP7 并促进 NLP7 从细胞质转移至细胞核中，该过程依赖于 Ca^{2+}，CPK28 对 NLP7 的磷酸化是低温下 NLP7 进核和调控植物低温应答所必需。RNA-seq 和 Chip-seq 结果表明，NLP7 调控大量冷响应基因的表达，其中部分冷响应基因的表达依赖于 Ca^{2+}。上述结果表明，NLP7 作用于 CPK28 下游解码低温特异 Ca^{2+}信号并调控冷响应基因的表达。NLP7 是植物响应氮信号的关键转录因子。先前研究报道，CPK10、CPK30 和 CPK32 在细胞核中磷酸化 NLP7 第 205 位 Ser，使其滞留在细胞核中，进而激活氮应答基因的表达。我们发现，低温激活的 CPK28 磷酸化 NLP7 的第 783、793、807、808 位 Ser 和第 817 位 Thr，促进细胞质定位的 NLP7 转移至细胞核中，由不同的 CPK 成员磷酸化 NLP7 产生的不同磷酸化密码，在植物应答不同环境信号中发挥重要作用。该研究不仅解析了植物感知和应答低温特异 Ca^{2+}信号的分子机理，还阐释了低温信号快速从细胞膜传递至细胞核的分子机制（Ding et al., *Sci Adv*, 2022）。论文发表后， *Nature Plants* 杂志发表题为“Decoding cold-induced Ca^{2+} spikes”的 research highlights 专评，该文还被 F1000 推荐。

CPK28-NLP7 Module Integrates Cold-Induced Ca^{2+} Signal and Transcriptional Reprogramming in *Arabidopsis*

Exposure to cold triggers a spike in cytosolic calcium (Ca^{2+}) that often leads to transcriptional reprogramming in plants. However, how this Ca^{2+} signal is perceived and relayed to the downstream cold signaling pathway remains unknown.Here, we show that the CALCIUM-DEPENDENT PROTEIN KINASE 28 (CPK28) initiates a phosphorylation cascade to specify transcriptional reprogramming downstream of cold-induced Ca^{2+} signal.Plasma membrane (PM)-localized CPK28 is activated rapidly upon cold shock within 10 seconds in a Ca^{2+}-dependent manner. CPK28 then phosphorylates and promotes the nuclear translocation of NIN-LIKE PROTEIN 7 (NLP7), a transcription factor that specifies the transcriptional reprogramming of cold-responsive gene sets in response to Ca^{2+}, thereby positively regulating plant response to cold stress. This study elucidates a previously unidentified mechanism by which the CPK28-NLP7 regulatory module integrates cold-evoked Ca^{2+} signal and transcriptome and thus uncovers a key strategy for the rapid perception and transduction of cold signals from the PM to the nucleus (Ding

et al., *Sci Adv,* 2022).

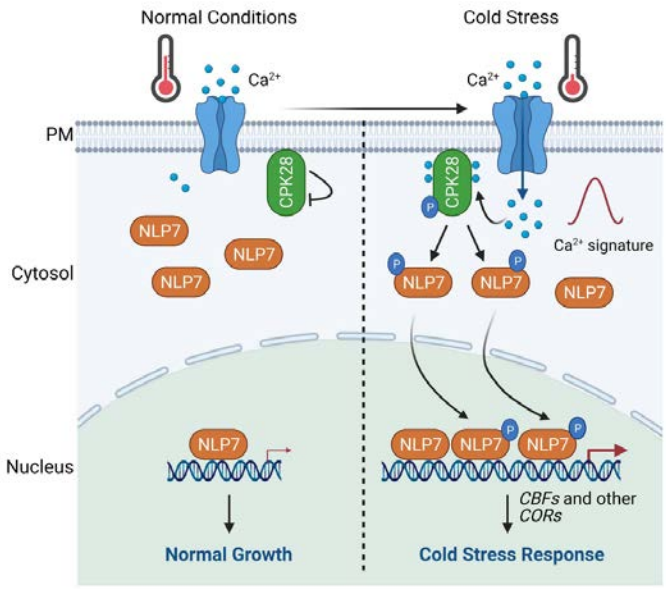


图 3、CPK28-NLP7 模块介导低温诱导的钙信号感知和解码的分子模型。

Figure 3. Working model for CPK28-NLP7 in cold-induced Ca^{2+} signature sensing and transduction.

（二） 研究成果

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

1. Jiang H#, Shi Y#, Liu J#, Li Z#, Fu D, Wu S, Li M, Yang Z, Shi Y, Lai J, Yang X, Gong Z, Hua J, **Yang S*** (2022) Natural polymorphism of *ZmICE1* contributes to amino acid metabolism that impacts cold tolerance in maize. ***Nat Plants*** 8: 1176-1190.
2. Ding Y#,*, Yang H#, Wu S, Fu D, Li M, Gong Z, **Yang S*** (2022) CPK28–NLP7 module integrates cold-induced Ca^{2+} signal and transcriptional reprogramming in *Arabidopsis*. ***Sci Adv*** 8: eabn7901. (Highlighted with a Research Highlights in *Nat Plants*; Selected for F1000 Prime)
3. Li Z, Fu D, Wang X, Zhang X, Tian J, Zhang S, Yang X, Tian F, Lai J, Shi Y*, **Yang S*** (2022) The transcription factor bZIP68 negatively regulates cold tolerance in maize. ***Plant Cell*** 34: 2833-2851. (Highlighted with In Brief in *Plant Cell*)
4. Ding Y*, **Yang S*** (2022) Surviving and thriving: How plants perceive and respond to temperature stress. ***Dev Cell*** 57: 947-958.
5. Sun Z, Feng Z, Ding Y, Qi Y, Jiang S, Li Z, Wang Y, Qi J, Song C, **Yang S**, Gong Z* (2022) RAF22, ABI1 and OST1 form a dynamic interactive network that optimizes plant growth and responses to drought stress in *Arabidopsis*. ***Mol Plant*** 15: 1192-1210.
6. Qi L#, Shi Y#, Terzaghi W, **Yang S***, Li J* (2022) Integration of light and temperature signaling

pathways in plants. ***J Integr Plant Biol*** 64: 393-411.

7. Song P, Yang Z, Guo C, Han R, Wang H, Dong J, Kang D, Guo Y, **Yang S**, Li J* (2022) 14-3-3 proteins regulate photomorphogenesis by facilitating light-induced degradation of PIF3. ***New Phytol*** doi: 10.1111/nph.
8. **Yang S*** (2022) Cold responses in rice: From physiology to molecular biology. ***J Plant Physiol*** 269: 153602.
9. Pei D, Hua D, Deng J, Wang Z, Song C, Wang Y, Wang Y, Qi J, Kollist H, **Yang S**, Guo Y, Gong Z* (2022) Phosphorylation of the plasma membrane H^+-ATPase AHA2 by BAK1 is required for ABA-induced stomatal closure in *Arabidopsis*. ***Plant Cell*** 34: 2708-2729.
10. Deng J, Kong L, Zhu Y, Pei D, Chen X, Wang Y, Qi J, Song C, **Yang S**, Gong Z* (2022) BAK1 plays contrasting roles in regulating abscisic acid-induced stomatal closure and abscisic acid-inhibited primary root growth in *Arabidopsis*. ***J Integr Plant Biol*** 64: 1264-1280.

授权专利：

1. 玉米 MYB39 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用。申请人：**杨淑华**，**施怡婷**，**张晓燕**；专利号: ZL201911402494.5；授权日期: 2022 年 09 月 06 日。
2. 玉米 CRR1 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用。申请人：**杨淑华**，曾榕，**张晓燕**；专利号: ZL201911421824.5；授权日期: 2022 年 09 月 06 日。
3. ZmbZIP68 蛋白及其编码基因在调控玉米耐受低温胁迫中的应用。申请人：**杨淑华**，**施怡婷**，李卓洋；专利号: ZL201911325467.2；授权日期: 2022 年 07 月 15 日。
4. 玉米耐低温基因 *ZmCIPK10.1* 在提高植物耐寒性中的应用。申请人：**杨淑华**，**施怡婷**，**张晓燕**；专利号: ZL201911319236.0；授权日期: 2022 年 07 月 19 日。

（三） 研究队伍

固定人员：

杨淑华（课题组长），张晓燕，施怡婷，丁杨林。

博士后：王西，曾榕。

研究生：

傅迪毅，明宇航，彭悦，高磊，林启红，宋悦，吴时凤，张晓瑞，王坤，李静，李岷泽，廖欢，宫玥，江圣哲，田志远，郑善公，陈家乐，游鹏，任柯宇，王潇，张卓。

郭　岩

课题组

郭岩，教授。

研究方向：植物感受与响应盐碱胁迫信号的分子调控机制。

（一） 研究进展

1、SOS1 的负调控元件——磷酸酶 PP2C D6/D7 响应盐胁迫的调控机制

盐胁迫是制约植物生长的最主要非生物胁迫之一。SOS 信号通路是植物中重要和保守的抗盐信号通路。植物感受外界盐胁迫，细胞内产生特异的钙信号，其被感受器 SOS3 及 SCaBP8 接收解码并传递给下游激酶 SOS2，激活 SOS2 的同时将 SOS2 招募到细胞质膜上磷酸化位于质膜上的 Na^+/H^+离子转运体 SOS1，激活 SOS1 的 Na^+离子外排活性，以此维持植物体内的离子平衡，帮助植物抵抗盐胁迫。SOS1 磷酸化水平的调控对于植物抵抗盐胁迫极其重要。底物的磷酸化水平由激酶以及磷酸酶共同调节，然而，目前针对 SOS1 只发现了激酶对它的磷酸化修饰，可以对其进行有效的去磷酸化修饰的磷酸酶尚未被报道。

该研究首次发现了 SOS1 的一类负调控元件，D 类 PP2C 磷酸酶 D6 和 D7。他们可以依赖自身磷酸酶活性在正常情况下抑制 SOS1 活性。盐胁迫下钙信号感受器 SCaBP8 结合钙离子后抑制 PP2C D6 和 D7 的活性，同时调节 PP2C 自质膜解离到胞质，以此解除 PP2C 对 SOS1 的抑制，使 SOS1 可以被活性，帮助植物抗盐。该研究从互作筛选入手，找到了两个与 SOS1 相互作用的磷酸酶 PP2C D6 和 D7，并经过表型观察以及生理活性检测确定了这两个磷酸酶对于 SOS1 的负调控作用。对这两个 PP2C 的活性检测以及相关遗传材料表型观察的结果表明，PP2C D6 和 D7 依赖自身的磷酸酶活性，在正常情况（非胁迫条件）下抑制了 SOS1 的活性，使 SOS 途径维持在低活状态。研究人员又针对胁迫条件下 PP2C D6 和 D7 对 SOS1 的抑制是如何被调控的进行了深入的探索，发现盐胁迫下 SCaBP8 在钙信号的介导下与 PP2C.D6 相互作用，相关活性检测实验证明盐胁迫下 SCaBP8 抑制了 PP2C.D6 的磷酸酶活性。进一步的细胞学观察发现，PP2C.D6 的亚细胞定位在盐胁迫下发生了有趣的变化，呈现出一种由质膜向胞质迁移的现象，并且 PP2C.D6 这种胁迫下的定位变化也是由 SCaBP8 所调控的。最终的遗传数据说明，盐胁迫下 SCaBP8 通过对 PP2C 的活性以及亚细胞定位的调控解除了 PP2C 对 SOS1 的抑制。综上，该研究首次证实磷酸酶 PP2C D6 和 D7 作为 SOS1 的负调控元件，在正常情况下抑制 SOS1。盐胁迫下的特异钙信号经 SCaBP8 解码，一方面通过激酶 SOS2 激活 SOS1，另一方面解除磷酸酶 PP2C D6 及 D7 对 SOS1 的抑制，在两个方向上正调控 SOS1 的活性，帮助植物更好的抵抗盐胁迫。该研究成果于 2022 年 3 月在《*Plant Cell*》

上以长文形式发表（Fu et al., *Plant Cell*, 2022）。

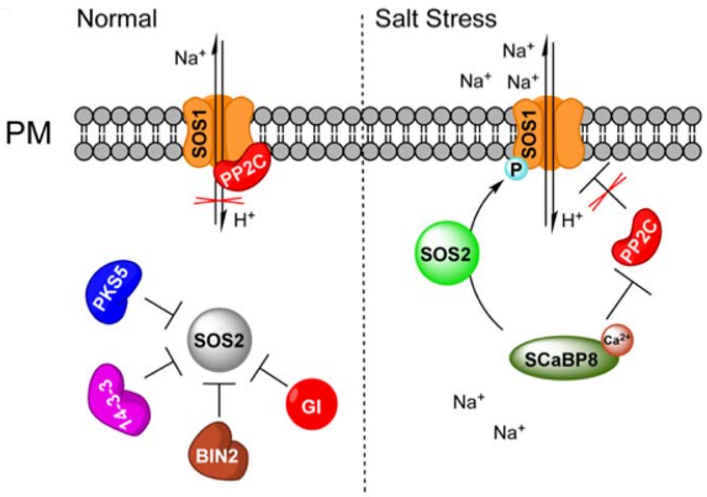


图 1、磷酸酶 PP2C D6/D7 调控植物响应盐胁迫的分子模型。

Figure 1. A working model for PP2C D6/D7-mediated plant salt tolerance.

SALT OVERLY SENSITIVE 1 is Inhibited by Clade D Protein Phosphatase 2C D6 and D7 in *Arabidopsis thaliana*

The salt overly sensitive (SOS) pathway is essential for maintaining sodium ion homeostasis in plants. This conserved pathway is activated by a calcium signaling-dependent phosphorylation cascade. However, the identity of the phosphatases and their regulatory mechanisms that would deactivate the SOS pathway remain unclear. In this study, we demonstrate that PP2C.D6 and PP2C.D7, which belong to clade D of the protein phosphatase 2C (PP2C) subfamily in *Arabidopsis thaliana*, directly interact with SOS1 and inhibit its Na^+/H^+ antiporter activity under non-salt-stress conditions. Upon salt stress, SOS3-LIKE CALCIUM-BINDING PROTEIN8 (SCaBP8), a member of the SOS pathway, interacts with the PP2Cs and suppresses their phosphatase activity; simultaneously, SCaBP8 regulates the subcellular localization of PP2C.D6 by releasing it from the plasma membrane. Thus, we identified two negative regulators of the SOS pathway that repress SOS1 activity under nonstress conditions. These processes set the stage for the activation of SOS1 by the kinase SOS2 to achieve plant salt tolerance. Our results suggest that reversible phosphorylation/dephosphorylation is crucial for the regulation of the SOS pathway, and that calcium sensors play dual roles in activating/deactivating SOS2 and PP2C phosphatases under salt stress (Fu et al., *Plant Cell*, 2022).

2、质膜 H^+-ATPase 抑制剂验证生长素极性运输模型

植物激素生长素（吲哚-3-乙酸[IAA]）在植物的生长发育中起着十分重要的作用，但它功能的发挥依赖于其跨细胞的极性运输。从上世纪七十年代，Rubery 等科学家提出了解释生长素极性运输的模型-化学渗透极性扩散假说（Rubery 和 Sheldrake，1974），该假说认为生长素极性运输依赖于质

膜 H^+-ATPase 建立的跨膜质子梯度。由于 IAA 是一种弱酸（pKa4.85），部分（17%）质子化 IAA 存在于酸性质外体（pH 5.5-5.7），使其更容易通过亲脂性脂质双层扩散到细胞质中。然而，在偏碱性的细胞内部（pH7.0-7.4），IAA 的质子化形式几乎完全解离，产生阴离子 IAA，它无法扩散出细胞。在这种情况下，负责建立跨质膜质子梯度的质膜 H^+-ATPase 可能在驱动生长素的极性转运中起关键作用。但是，到目前为止，质膜 H^+-ATPase 是否参与生长素的极性运输仍然缺乏直接的遗传证据，主要是由于 PM *H^+-ATPase* 基因家族成员的功能冗余。例如，在模式植物拟南芥中，PM *H^+-ATPase* 基因家族包含 11 个成员（*AHA1* 到 *AHA11*），但是，相对于野生型，单个基因的突变不会导致生长素控制的植物生长发育表型，而遗传失活该家族中的两个基因，例如 *aha1 aha2* 双突变体是胚胎致死的。该研究通过筛选一个小分子化合物库，发现一个可以选择性抑制 PM H^+-ATPase 活性的小分子 Protonstatin-1（PS-1）。PS-1 与 PM H^+-ATPase 胞内 central loop 相互作用并抑制 PM H^+-ATPase 活性。利用 PS-1 为研究工具发现，PS-1 抑制 PM H^+-ATPase 活性后，影响了拟南芥体内生长素的极性运输和生长素极性运输介导的表型。研究结果为化学渗透极性扩散假说提供了实验证据，表明 PM H^+-ATPase 在极性生长素转运中起着十分重要的作用。该研究成果于 2022 年 3 月在《*J Integr Plant Biol*》上以长文形式发表（Yang et al., *J Integr Plant Biol*, 2022）。

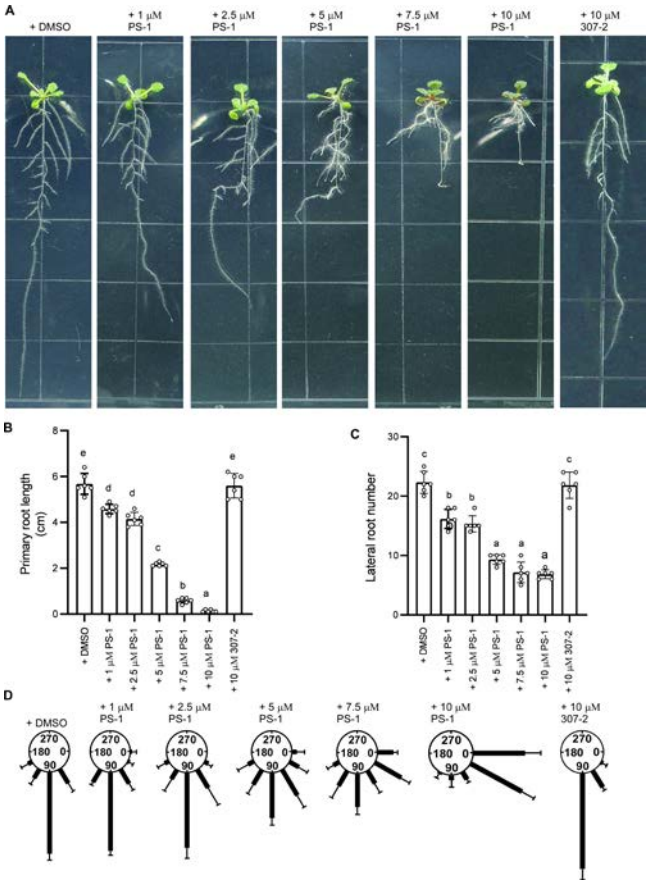


图2、PS-1抑制生长素极性运输。

Figure 2. PS-1 affects auxin-controlled seedlings growth in *Arabidopsis*.

Testing the Polar Auxin Transport Model with a Selective Plasma Membrane H^+-Atpase Inhibitor

Auxin is unique among plant hormones in that its function requires polarized transport across plant cells. A chemiosmotic model was proposed to explain how polar auxin transport is derived by the H^+ gradient across the plasma membrane established by plasma membrane H^+-ATPases (PM H^+-ATPases). However, a classical genetic approach by mutations in PM H^+-ATPase members did not result in the ablation of polar auxin distribution, possibly due to functional redundancy in this gene family. To confirm the crucial role of PM H^+-ATPases in the polar auxin transport model (PATM), we employed a chemical genetic approach. Through a chemical screen, we identified protonstatin-1 (PS-1), a selective small-molecule inhibitor of PM H^+-ATPase activity that inhibits auxin transport. Assays with transgenic plants and yeast strains showed that the activity of PM H^+-ATPases affects auxin uptake as well as acropetal and basipetal polar auxin transport. We propose that PS-1 can be used as a tool to interrogate the function of PM H^+-ATPases. Our results support the chemiosmotic model in which PM H^+-ATPase itself plays a fundamental role in polar auxin transport.

（二） 研究成果

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

1. Fu H, Yu X, Jiang Y, Wang Y, Yang Y, Chen S, Chen Q, **Guo Y*** (2022) SALT OVERLY SENSITIVE 1 is inhibited by clade D protein phosphatase 2C D6 and D7 in *Arabidopsis thaliana*. ***Plant Cell*** 23: koac283.
2. **Yang Y#,***, Liu X#, Guo W, Liu W, Shao W, Zhao J, Li J, Dong Q, Ma L, He Q, Li Y, Han J, Lei X* (2022) Testing the polar auxin transport model with a selective plasma membrane H^+-ATPase inhibitor. ***J Integr Plant Biol*** 64:1229-1245.

（三） 研究队伍

固定人员：

郭岩（课题组长），杨永青，李景睿。

研究生：

刘香凝，邵征宇，白栎，孙丽萍，李钦沛，霍彦丹，罗曼卿，石晓晨，汪蓉，许可心，张璐璐，马直先，倪徐平，刘冬旭，赵俊丹，张东民，刘晓，张红艳，段晓蕾，周红阳。

巩志忠

课题组

巩志忠，教授。

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、ABA 诱导的气孔关闭质膜 H^+-ATPase AHA2 被 BAK1 磷酸化

光激活质膜定位质子 ATP 酶（PM H^+-ATPase）在很大程度上促进了气孔的开放。在干旱胁迫下，气孔关闭主要受脱落酸（ABA）调节。目前尚不清楚 PM H^+-ATPse 是否参与 ABA 诱导的气孔关闭。通过对拟南芥干旱处理表型观察，以及叶片含水量和离体叶片失水率等生理指标测定，鉴定到 ABA 诱导的气孔关闭的正调控因子 PM *Arabidopsis* H^+ -ATPase isoform 2（AHA2）。研究发现, AHA2 与蛋白激酶 BRI1-ASSOCIATED RECEPTOR KINASE 1（BAK1）相互作用，ABA 增强 BAK1 对 AHA2-C 末端 Ser944 残基的磷酸化从而正调控 AHA2 的活性，导致 H^+快速流出、细胞质碱化和活性氧（ROS）积累，从而启动 ABA 信号转导，引起气孔关闭。研究表明，AHA2 在植物对干旱胁迫的响应过程中对细胞质碱化和 ABA 诱导的气孔关闭起到关键作用（Pei et al. , *Plant Cell*, 2022）。

Phosphorylation of the Plasma Membrane H^+-Atpase AHA2 by BAK1 is Required for ABA-Induced Stomatal Closure in *Arabidopsis*

Stomatal opening is largely promoted by light-activated plasma membrane-localized proton ATPases (PM H^+ -ATPases), while their closure is mainly modulated by abscisic acid (ABA) signaling during drought stress. It is unknown whether PM H^+- ATPases participate in ABA-induced stomatal closure. We established that BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) interacts with, phosphorylates and activates the major PM *Arabidopsis* H^+ -ATPase isoform 2 (AHA2). ABA-activated BAK1 phosphorylated AHA2 at Ser-944 in its C-terminus and activated AHA2, leading to rapid H^+ efflux, cytoplasmic alkalinization, and reactive oxygen species (ROS) accumulation, to initiate ABA signal transduction and stomatal closure. The phosphorylation-mimicking mutation $AHA2^{S944D}$ driven by its own promoter could largely compensate for the defective phenotypes of water loss, cytoplasmic alkalinization, and ROS accumulation in both *aha2-6* and *bak1-4* mutants. Our results uncover a crucial role of AHA2 in cytoplasmic alkalinization and ABA-induced stomatal closure during the plant's response to drought stress (Pei et al. , *Plant Cell*, 2022).

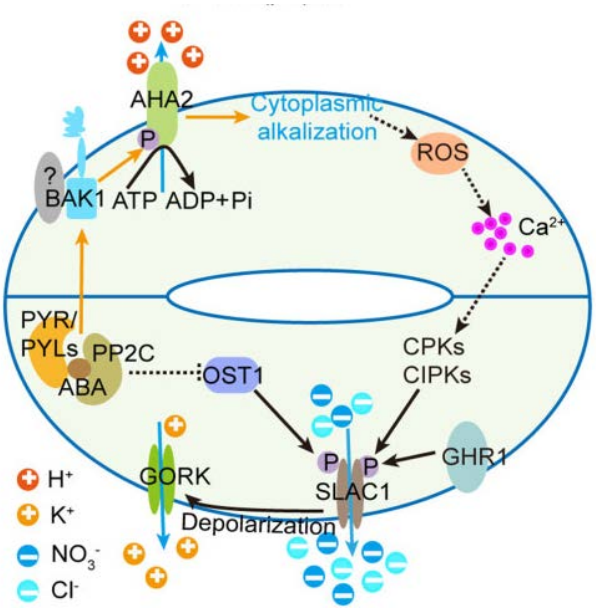


图1、ABA诱导气孔关闭中BAK1介导的AHA2激活的分子模型。

Figure 1. Proposed model of BAK1-mediated AHA2 activation during ABA-induced stomatal closure.

2、拟南芥 RAF22，ABI1 和 OST1 形成动态互作网络优化植物生长和旱胁迫响应

干旱胁迫诱导植物激素脱落酸（ABA）的积累，触发 ABA 信号传导，然而，植物正常生长和胁迫响应之间切换的分子机制仍不清楚。通过筛选具有抗旱或旱敏感表型的拟南芥突变体，鉴定到响应干旱胁迫的负调控因子 RAF（rapidly accelerated fibrosarcoma）- LIKE MITOGEN-ACTIVATED PROTEIN KINASE KINASE KINASE 22（RAF22）。研究发现，RAF22 与 ABA 信号通路的重要组分 ABA INSENSITIVE1（ABI1）相互作用，RAF22 磷酸化 ABI1 的 Ser416 残基，增强了 ABI1 的磷酸酶活性。进一步研究发现，ABI1 还可以通过去磷酸化 RAF22 来增强 RAF22 的激酶活性，从而相互抑制 ABA 信号传导，促进植物在正常条件下的生长。在干旱胁迫下，ABA 激活的蛋白激酶 OPEN STOMATA1（OST1）磷酸化 RAF22 的 Ser81 残基并抑制其激酶活性，抑制其对 ABI1 磷酸酶活性的增强。研究表明，RAF22、ABI1 和 OST1 形成了一个动态调控网络，在优化植物生长和环境适应方面发挥着关键作用（Sun et al. , *Mol Plant*, 2022）。

RAF22, ABI1 and OST1 Form a Dynamic Interactive Network That Optimizes Plant Growth and Responses to Drought Stress in *Arabidopsis*

Drought stress induces accumulation of the plant hormone abscisic acid (ABA), triggering ABA signal transduction. However, the molecular mechanisms for switching between plant growth promotion and stress response remain poorly understood. Here we report that RAF (rapidly accelerated fibrosarcoma) -LIKE MITOGEN-ACTIVATED PROTEIN KINASE KINASE KINASE 22 (RAF22) in *Arabidopsis thaliana* physically interacts with ABA INSENSITIVE 1 (ABI1) and phosphorylates ABI1 at Ser416 residue to enhance its phosphatase activity. Interestingly, ABI1

can also enhance the activity of RAF22 through dephosphorylation, reciprocally inhibiting ABA signaling and promoting the maintenance of plant growth under normal conditions. Under drought stress, however, the ABA-activated OPEN STOMATA1 (OST1) phosphorylates the Ser81 residue of RAF22 and inhibits its kinase activity, restraining its enhancement of ABI1 activity. Taken together, our study reveals that RAF22, ABI1, and OST1 form a dynamic regulatory network that plays crucial roles in optimizing plant growth and environmental adaptation under drought stress (Sun et al. , *Mol Plant*, 2022).

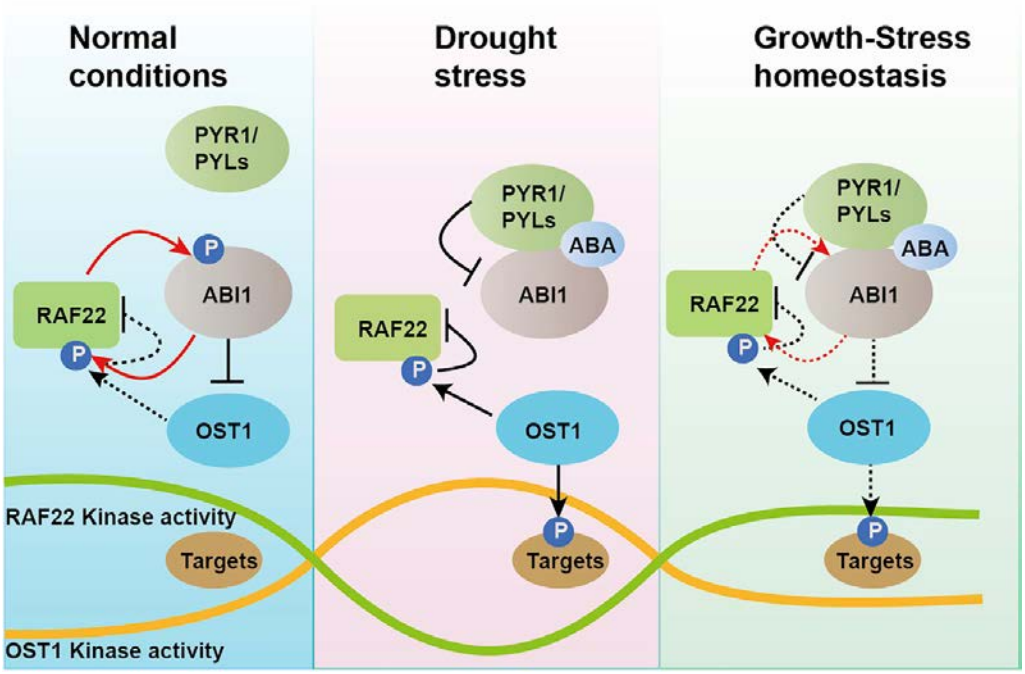


图 2、RAF22, ABI1 和 OST1 在植物中形成的动态互作网络模型。

Figure 2. A proposed model illustrating how the dynamic interactive network formed by RAF22, ABI1, and OST1 works in plants.

（二） 研究成果

发表论文：（*Corresponding author）

1. Pei D, Hua D, Deng J, Wang Z, Song C, Wang Y, Wang Y, Qi J, Kollist H, Yang S, Guo Y, **Gong Z*** (2022) Phosphorylation of the plasma membrane H^+-ATPase AHA2 by BAK1 is required for ABA-induced stomatal closure in *Arabidopsis*. ***Plant Cell*** 34: 2708-2729.
2. Deng J, Kong L, Zhu Y, Pei D, Chen X, Wang Y, Qi J, Song C, Yang S and **Gong Z*** (2022) BAK1 plays contrasting roles in regulating abscisic acid‐induced stomatal closure and abscisic acid inhibited primary root growth in *Arabidopsis*. ***J Integr Plant Biol*** 64: 1264-1280.
3. Sun Z, Feng Z, Ding Y, Qi Y, Jiang S, Li Z，Wang Y, Qi J, Song C, Yang S and **Gong Z*** (2022) RAF22, ABI1 and OST1 form a dynamic interactive network that optimizes plant growth and responses to drought stress in *Arabidopsis*. ***Mol Plant*** 15: 1192–1210.

专利授权：

1. DRK蛋白及其编码基因在植物抗旱中的应用。申请人：**巩志忠**，**王瑜**，孙志慧；专利号：ZL202011003964.3；授权日期：2022年04月12日。
2. 玉米*CPK2*基因在植物抗旱中的应用。申请人：**巩志忠**，**王瑜**，胡晓莹；专利号：ZL202010930137.2；授权日期：2022年02月08日。
3. PP84蛋白及其编码基因在调控植物抗旱性中的应用。申请人：**王瑜**，**巩志忠**，郭亚真；专利号：ZL201911417842.6；授权日期：2022年04月05日。
4. GLK7蛋白及其编码基因在植物抗旱中的应用。申请人：**王瑜**，**巩志忠**，杨欣欣；专利号：ZL202011005398.X；授权日期：2022年05月17日。

（三） 研究队伍

固定人员：

巩志忠（课题组长），齐俊生，王瑜，程金魁。

研究生：

綦元鹏，房婷婷，韩祎楠，杨欣欣，陈慧，蒋杉，王婷婷，唐冬雪，李静蓉，冯贞凯，卢敏敏，朱燕妮，钟自婷，马赫，麦健涛，李慧颖，董雪莹，李瑞，赵雯莉，张越美，曹润霖。

傅　缨

课题组

傅缨，教授。

研究方向：（1）细胞骨架响应植物体内生长发育信号调控细胞极性生长的机制研究；（2）细胞骨架响应环境信号调控细胞生长和气孔运动的机制研究。

（一） 研究进展

1、拟南芥 SYP121 作为 ROP2 效应因子调控根毛顶端生长的机制研究

顶端生长是细胞极性扩张的一种极端形式，一些具有特殊功能的真核细胞采用这种生长模式形成高度伸长的管状，包括真菌菌丝，动物神经细胞，植物的花粉管和根毛等。根毛是从根表皮细胞突出的管状结构，利于水分、养分的吸收，与微生物的互作以及植物的固着。根毛的顶端生长需要将囊泡极性运输到顶端生长位点和活跃的胞吐作用。然而，根毛顶端的胞吐是如何被时空调控的仍需深入解析。本研究发现 Qa-SNARE（Soluble *N*-ethylmaleimide-sensitive factor attachment protein receptor）SYP121 是植物小 G 蛋白 ROP2 的效应因子，参与 ROP2 信号途径对根毛顶端生长的调控。有活性的 ROP2 促进 SYP121 在根毛顶端质膜的极性分布，并且 ROP2 与 SYP121 直接结合。进一步的研究发现 ROP2 与 SYP121 的互作可以解除 Sec1/Munc18 蛋白 SEC11 对 SYP121 功能的抑制作用，利于 SYP121 与 R-SNARE VAMP722 之间相互作用形成 SNARE 复合体，进而促进了根毛顶端的胞吐作用。本研究发现了 ROP 信号途径与囊泡运输间的直接联系，并揭示了 ROP 小 G 蛋白通过调控 SNARE 复合体的组装以及 SNARE 蛋白的极性定位，从而调控细胞中极性胞吐作用的分子机制（Cui et al., *Mol Plant*, 2022）。

Arabidopsis SYP121 Acts as an ROP2 Effector in the Regulation of Root Hair Tip Growth

Tip growth is an extreme form of polarized cell expansion occurring in all eukaryotic kingdoms to generate highly elongated tubular cells with specialized functions, including fungal hyphae, animal neurons, plant pollen tubes, and root hairs (RHs). RHs are tubular structures protruding from the root epidermis to facilitate water and nutrient uptake, microbial interactions, and plant anchorage. RH tip growth requires localized vesicle-targeting and active exocytosis at apical growth sites. However, how apical exocytosis is spatially and temporally controlled during tip growth remains elusive. Here, we report that the Qa-Soluble *N*-ethylmaleimide-sensitive factor attachment protein receptor (SNARE) SYP121 acts as an effector of Rho of Plants 2 (ROP2), mediating regulation of RH tip growth. We show that active ROP2 promotes SYP121 targeting to

the apical plasma membrane. Moreover, ROP2 directly interacts with SYP121 and promotes the interaction between SYP121 and the R-SNARE VAMP722 to form a SNARE complex, likely by counteracting with the Sec1/Munc18 protein SEC11 which suppresses SYP121's function. Thus, the ROP2-SYP121 pathway facilitates exocytic trafficking during RH tip growth. This study uncovers a direct link between a ROP GTPase and vesicular trafficking and a new mechanism controlling apical exocytosis, whereby ROP GTPase signaling spatially regulates SNARE complex assembly and the polar distribution of a Q-SNARE (Cui et al., *Mol Plant*, 2022).

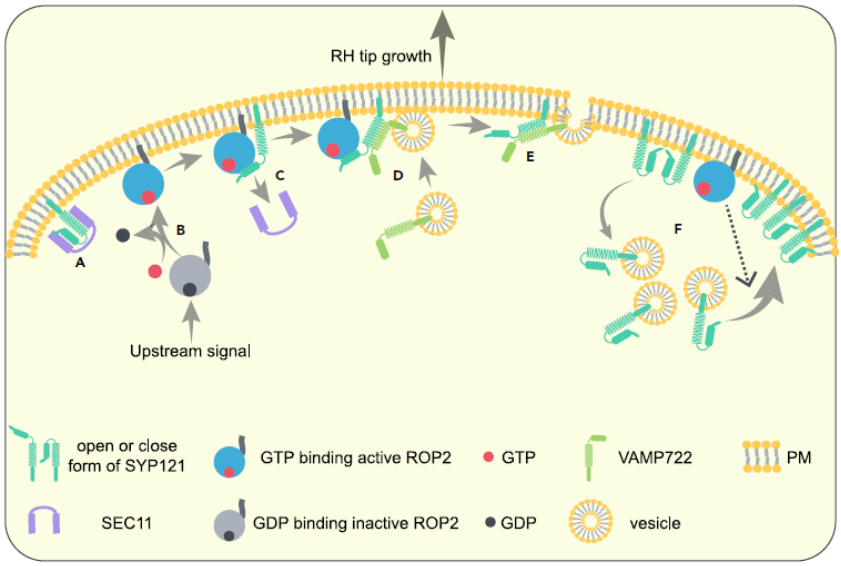


图 1、ROP2-SYP121 调控根毛生长的工作模式图。

Figure 1. A hypothetical model of the ROP2-SYP121 pathway in the regulation of root hair tip growth.

2、拟南芥微管驱动蛋白 ARK2 稳定微管正端并促进微管成束的分子机制研究

微管的动态变化和组织对于植物细胞的形态建成非常重要。驱动蛋白是一类以微管为轨道，在细胞中执行众多生物学功能的分子马达。之前的研究表明，驱动蛋白除了具有运输囊泡和膜性细胞器参与细胞分裂及信号传导等功能外，还参与了对微管的动态调控。然而在植物细胞中驱动蛋白如何调控微管动态和组织方式仍有待研究。ARMADILLO REPEAT KINESIN（ARK）是一个植物特有的驱动蛋白亚家族，在拟南芥中有三个成员（ARK1，ARK2，ARK3）。 ARK2 已被证明参与了根表皮细胞的形态发生。然而，ARK2 蛋白的生物学功能以及对微管的作用机制还不清楚。本研究证明了 ARK2 与周质微管共定位，在体外和体内都能促进微管束的形成。药理学实验和微管动力学分析表明，ARK2 能稳定周质微管。实时动态追踪观察发现， ARK2 可以沿周质微管前行，能在微管正端和侧壁定位。活细胞成像显示 *ARK2* 功能缺失后，突变体下胚轴细胞的周质微管密度降低，成束的微管显著减少，进一步说明 ARK2 参与调控了周质微管列阵的组织排列。本研究证明了 ARK2 追踪并稳定正在生长的微管正端，促进了平行微管束的形成，并影响细胞的极性生长（Lan et al., *J Integr Plant Biol*, 2022）。

ARK2 Stabilizes the Plus-End of Microtubules and Promotes Microtubule Bundling in *Arabidopsis*

Microtubule dynamics and organization are important for plant cell morphogenesis and development. The microtubule-based motor proteins kinesins are mainly responsible for the transport of some organelles and vesicles, although several have also been shown to regulate microtubule organization. The ARMADILLO REPEAT KINESIN (ARK) family is a plant-specific motor protein subfamily that consists of three members (ARK1, ARK2, and ARK3) in *Arabidopsis thaliana*. ARK2 has been shown to participate in root epidermal cell morphogenesis. However, whether and how ARK2 associates with microtubules needs further elucidation. Here, we demonstrated that ARK2 co-localizes with microtubules and facilitates microtubule bundling in vitro and in vivo. Pharmacological assays and microtubule dynamics analyses indicated that ARK2 stabilizes cortical microtubules. Live-cell imaging revealed that ARK2 moves along cortical microtubules in a processive mode and localizes both at the plus-end and the sidewall of microtubules. ARK2 therefore tracks and stabilizes the growing plus-ends of microtubules, which facilitates the formation of parallel microtubule bundles (Lan et al., *J Integr Plant Biol*, 2022).

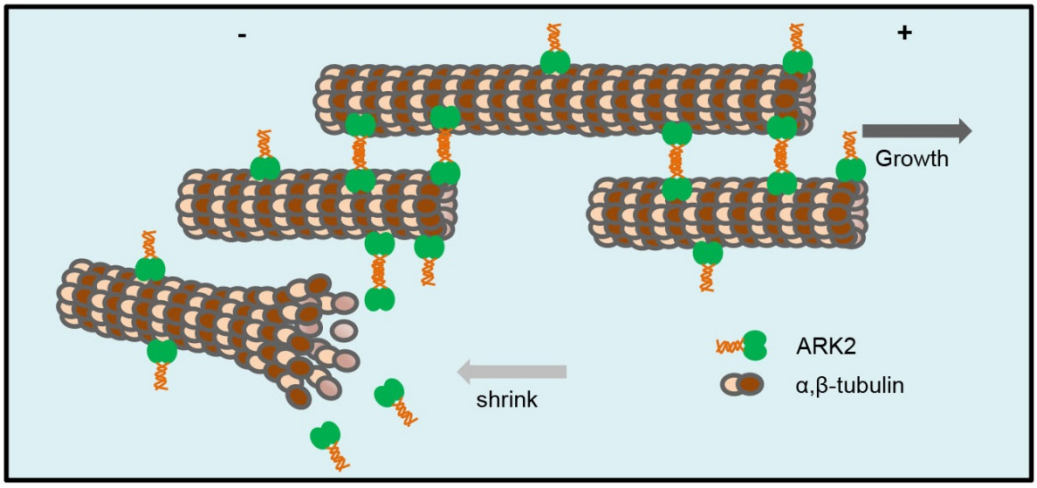


图 2、ARK2 稳定微管正端并促进平行微管成束的工作模型。

Figure 2. The hypothetical model of ARK2 involved in stabilizing microtubules and parallel microtubule bundle formation.

3、ARK2 参与光抑制拟南芥下胚轴伸长的机制研究

下胚轴在光照和黑暗条件下经历了不同的形态发生。细胞周质微管在光照下被重新定向以协调细胞的生长状态。本研究证明了微管驱动蛋白 ARMADILLO REPEAT KINESIN2（ARK2）负调控了拟南芥下胚轴的伸长生长。*ark2* 敲除突变体的下胚轴细胞比野生型的长，并且有相对更多的横向排列的周质微管。此外，ARK2 与周质微管共定位，在光照条件下蛋白稳定，促进了光诱导的周质微

管阵列的重新定向，参与了光对下胚轴伸长的抑制。进一步研究发现，ARK2 蛋白在黑暗中则通过 26S 蛋白体途径被降解。进一步研究发现 ARK2 可以与 E3 泛素连接酶 CONSTITUTIVE PHOTOMORPHOGENIC 1（COP1）相互作用，COP1 介导了 ARK2 在黑暗中的蛋白降解，从而有利于黄化下胚轴的生长（Lan et al., *J Exp Bot*, 2022）。

Stable ARMADILLO REPEAT KINESIN 2 in Light Inhibits Hypocotyl Elongation and Facilitates Light-Induced Cortical Microtubule Reorientation in *Arabidopsis*

Hypocotyls undergo different morphogenesis according to light and dark conditions. Cortical microtubules are reoriented in response to light to coordinate cell growth status. Kinesins are microtubule-based motor proteins that are mostly responsible for transporting organelles and vesicles, although some can also regulate microtubule organizations. However, whether kinesin can be involved in microtubule reorientation and hypocotyl elongation remains to be studied. Here, we demonstrated that ARMADILLO REPEAT KINESIN2 (ARK2) negatively regulated the hypocotyl elongation of *Arabidopsis thaliana*. The hypocotyl cells of the *ark2* null allele were longer than those of the wild type and had relatively more transversely arranged cortical microtubules. Moreover, ARK2 co-localized with cortical microtubules and facilitated the light-induced reorientation of the cortical microtubule arrays. Interestingly, ARK2 protein is stable in the light and degraded through 26S proteasome pathway in the dark. Furthermore, we proved that ARK2 could interact with the E3 ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1), which contributed to the down-regulation of ARK2 in darkness that may benefit hypocotyl growth in the dark (Lan *et al*., *J Exp Bot*, 2022).

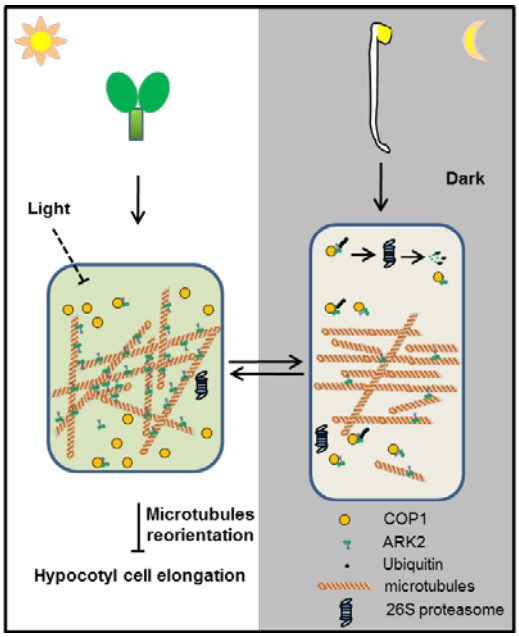


图 3、ARK2 调控光诱导的微管重新定向以抑制下胚轴伸长生长的工作模型。

Figure 3. Working model of ARK2 in the regulation of light-induced microtubule reorientation during hypocotyl cell elongation.

4、ZmMYB69 调控玉米秸秆中木质素合成的机制研究

玉米秸秆经过发酵和酶解可以生产清洁能源,带来经济效益。然而，次生细胞壁中的木质素含量会影响细胞壁中木质纤维素多糖的水解作用，进而影响玉米秸秆的转化利用效率。因此，通过生物技术方法改变木质素含量可以作为提高玉米生物质能源利用的一个重要策略。目前在拟南芥和一些木本植物中的研究发现了 NAC-MYB 介导的多级转录调控网络在木质素合成中的重要作用，尽管在玉米中已发现 ZmMYB31 和 ZmMYB42 抑制木质素合成基因的表达，但相关层级调控网络中的其它重要组分和调控机制仍所知甚少。本研究发现玉米 R2R3-MYB 类转录因子 ZmMYB69 的过量表达导致玉米秸秆中木质素含量降低、细胞壁变薄、株高也受到抑制；而 *ZmMYB69* 功能缺失突变体植株中木质素含量增加、细胞壁变厚，但株高与野生型没有明显差异。为解析 ZmMYB69 调控木质素合成的机制，通过原位 PCR 和利用酵母系统进行的研究发现，*ZmMYB69* 主要在维管束细胞表达，所编码的 ZmMYB69 蛋白具有转录激活活性。进一步通过染色质免疫共沉淀、凝胶阻滞和转录激活等实验证明 ZmMYB69 通过直接调节木质素合成途径中的两个转录抑制子 *ZmMYB31* 和 *ZmMYB42* 的表达进而参与对木质素合成的调控。此外，*ZmMYB69* 过量表达植株秸秆细胞壁的酶解效率显著增加。本研究不仅揭示了玉米木质素合成调控的新机制，还为通过生物技术方法提高玉米秸秆生物质能源生产提供了有用的线索（Qiang et al., *Plant Physiol*, 2022）。

The Transcription Factor ZmMYB69 Represses Lignin Biosynthesis by Activating ZmMYB31/42 Expression in Maize

Lignin is a phenylpropanoid-derived polymer that is directly deposited on the secondary walls of specialized cells, such as vessel elements and fibers, in plants. Lignification has vital roles in mechanical support, long-distance water transport, and plant defense. However, lignin is undesirable for biotechnological applications because its covalent interaction with cell wall polysaccharides limits the enzymatic digestion of agricultural biomass feedstocks. A hierarchical transcriptional network comprising various transcription factors (TFs), including NACs (NAM, ATAF and CUC) and MYBs (myeloblastosis-related proteins), controls lignin biosynthesis in *Arabidopsis thaliana*. In maize (*Zea mays* L.), ZmMYB31 and ZmMYB42 were repressors of lignin biosynthesis genes. However, the upstream regulation mechanism is still unrevealed. Here, we report that ZmMYB69 is a regulatory factor at the upper level of ZmMYB31 and ZmMYB42 in the hierarchical network that controls lignin biosynthesis in maize. We provide evidence that ZmMYB69 is a transcriptional activator and directly targets *ZmMYB31* and *ZmMYB42* promoters. Thereafter it can repress lignin biosynthesis by activating *ZmMYB31* and *ZmMYB42* expression. Moreover, the findings also implicate *ZmMYB69* as a good candidate for the manipulation of lignin biosynthesis in biotechnological applications (Qiang et al., *Plant Physiol*, 2022).

（二） 研究成果

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

1. Cui X#, Wang S#, Huang Y, Ding X, Wang Z, Zheng L, Bi Y, Ge F, Zhu L, Yuan M, Yalovsky S, **Fu Y*** (2022) *Arabidopsis* SYP121 acts as an ROP2 effector in the regulation of root hair tip growth. ***Mol Plant*** 15:1008-1023.
2. Li C#, Shi L#, Li X#, Wang Y, Bi Y, Li W, Ma H, Chen B, Zhu L, **Fu Y*** (2022) ECAP is a key negative regulator mediating different pathways to modulate salt stress-induced anthocyanin biosynthesis in *Arabidopsis*. ***New Phytol*** 233:2216-2231.
3. Qiang Z, Sun H, Ge F, Li W, Li C, Wang S, Zhang B, Zhu L, Zhang S, Wang X, Lai J, Qin F, Zhou Y, **Fu Y*** (2022) The transcription factor ZmMYB69 represses lignin biosynthesis by activating *ZmMYB31 /42* expression in maize. ***Plant Physiol*** 189:1916-1919.
4. Lan M, Liu X, Kang E, Fu Y, **Zhu L*** (2022) ARK2 stabilizes the plus-end of microtubules and promotes microtubule bundling in *Arabidopsis*. ***J Integr Plant Biol*** doi: 10.1111/jipb.13373. *Online*
5. Lan M, Kang E, Liu X, Fu Y, **Zhu L*** (2022) Stable ARMADILLO REPEAT KINESIN 2 in light inhibits hypocotyl elongation and facilitates light-induced cortical microtubule reorientation in *Arabidopsis*. ***J Exp Bot*** doi: 10.1093/jxb/erac473. *Online*

（三） 研究队伍

固定人员：

傅缨（课题组长），朱蕾，李长江。

博士后：石磊。

研究生：

李席，冯武韬，柳添元[1]（[1]朱蕾副教授所招学生），王莹莹，丁雪宁，李星，徐丽源[1]，郭鑫，孙洪华，刘夏楠[1]，吕高锋，景思豪，邹红宇，邢红杰[1]。

任东涛

课题组

任东涛，教授。

研究方向：植物逆境信号转导。

（一） 研究进展

1、拟南芥 AtPLC4 正调控细胞核钙信号响应盐胁迫的机制研究

钙离子（Ca^{2+}）是真核细胞中普遍存在的第二信使，参与诸多的生物和非生物胁迫响应过程。细胞质和细胞核是钙离子信号产生和解码的重要场所，目前大部分研究集中在胞质钙离子信号的解码，对于细胞核中钙离子信号的产生及解码却知之甚少。本课题组前期研究发现拟南芥磷脂酰肌醇特异性磷脂酶PLC4负调控盐胁迫响应，且胞质钙离子参与此调控过程。进一步研究发现盐胁迫导致PLC4在细胞核中富集，同时诱导核中Ca^{2+} 浓度的上升；*plc4*突变体抑制盐胁迫诱导的细胞核内钙离子浓度（$[Ca^{2+}]_{nuc}$）的上升，过表达*PLC4*导致盐诱导的$[Ca^{2+}]_{nuc}$的升高显著增强，而过表达*PLC4KL*（不入核形式）不能增强盐诱导的$[Ca^{2+}]_{nuc}$的升高。这些结果表明PLC4在细胞核中正调控盐诱导的$[Ca^{2+}]_{nuc}$的上升（图1）。该研究丰富了对核中钙信号系统的了解，为进一步阐明植物对逆境的响应过程特别是盐胁迫响应中钙信号的作用机制提供了更多的思路和理论依据。

AtPLC4 Positively Regulates Nuclear Calcium Signaling in Response to Salt Tolerance in *Arabidopsis*

As the signal molecule and the secondary messenger, the calcium ion is involved in many biotic and abiotic stresses in plants. The cytoplasm and nucleus are the important locations for the generation and decoding of intracellular calcium signal. Most of the current research focus on the decoding of cytoplasmic calcium ion signaling, while the discovery of calcium signal system in nucleus is also of great significance but little known. In this study, we found that PLC4 negatively regulates the response to salt stress, in which cytoplasmic calcium is involved. In addition, salt stress induced PLC4 expression in the nucleus and $[Ca^{2+}]_{nuc}$ elevation; inhibition of salt-stress-induced $[Ca^{2+}]_{nuc}$ elevation in *plc4* mutant was identified using FRET calcium imaging; overexpression of PLC4 resulted in a significant enhancement of the salt-induced increase in $[Ca^{2+}]_{nuc}$; however no obvious changes in nuclear Ca^{2+} induced by salt stress was observed in $PLC4^{K467L}$ (the non-nucleated PLC4) plants. These results indicates that PLC4 positively regulates the salt-induced rise of $[Ca^{2+}]_{nuc}$ in the nucleus, which enhancing our understanding of calcium

signals in the nucleus and providing more ideas and theoretical basis for future studies on plant responses to stress.

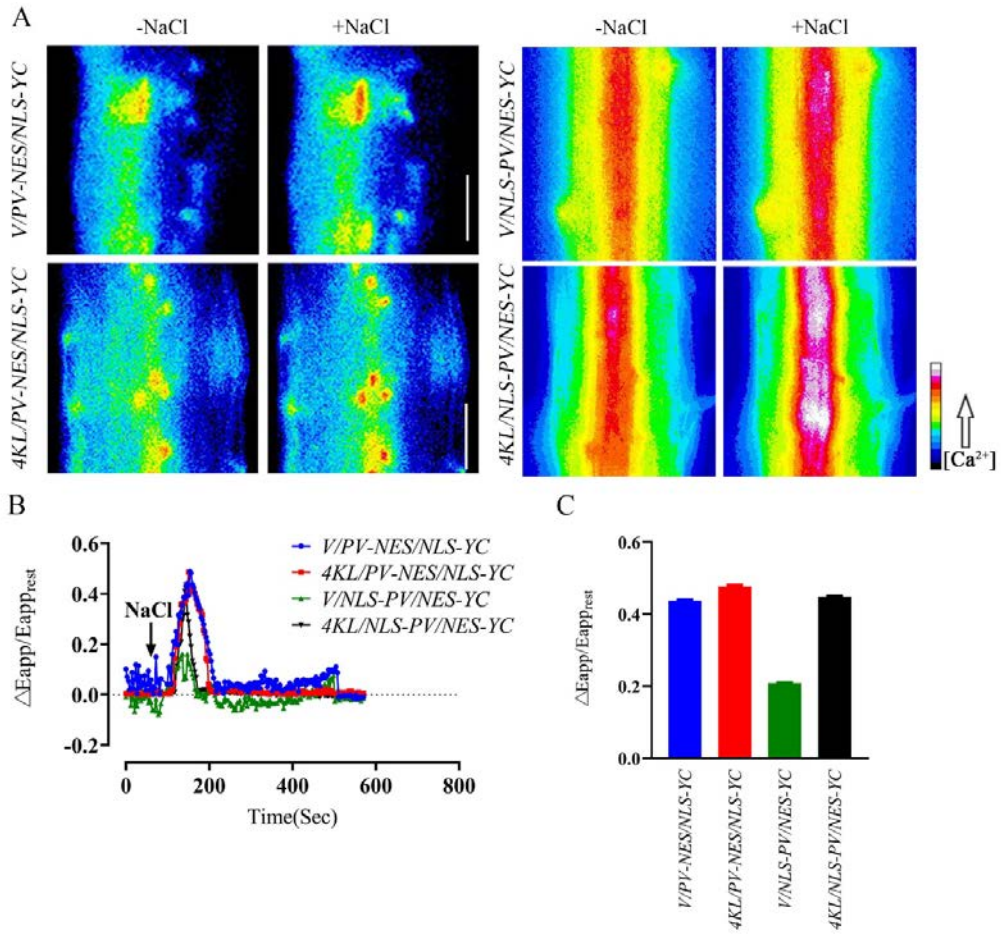


图1、过表达不入核PLC4不能增强盐诱导的$[Ca^{2+}]_{nuc}$的升高。

Figure 1. There is no obvious changes of salt-induced $[Ca^{2+}]_{nuc}$ increase in *PLC4K467L* plants.

2、MAPK 级联磷酸化 GSA1 负调控拟南芥原叶绿素酸酯含量的机制研究

幼苗的脱黄化过程指的是叶绿素合成以及变绿过程，这种转变是通过在暗下合成的原叶绿素酸酯见光后还原实现的。原叶绿素酸酯的过量积累会对植物产生光毒性，因此，在从暗到光的转变过程中，原叶绿素酸酯的适量积累以及快速转化对于幼苗的生存至关重要。本课题组前期研究发现 RAF35-MKK5-MPK6 级联通过抑制原叶绿素酸酯的积累参与拟南芥光形态建成，但是这一级联的下游底物及调控机制尚不清楚。本研究通过筛选叶绿素合成通路中的酶，发现催化 GSA 向 ALA 转化的催化酶 GSA1 在酵母中与 MPK6 互作并且在体外能够被 MPK6 磷酸化，BiFC 实验证明 GSA1 与 MPK6 在体内存在相互作用，暗示 GSA1 可能是 MPK6 的下游底物； *raf35*、*mkk5*、*mpk6* 和 *gsa1* 敲除突变体的黄化幼苗中原叶绿素酸酯的含量较 Col-0 明显升高，且 *gsa1* 见光后的存活能力明显增强。这些结果表明 RAF35-MKK5-MPK6 级联通过磷酸化 GSA1 负调控幼苗原叶绿素酸酯的含量，揭示了磷酸化修饰在调控叶绿素合成途径酶功能中重要作用，对进一步研究植物叶绿素合成途径的调控机制具有重要意义。

Phosphorylation of GSA1 by MAPK Cascade Negatively Regulates Protochlorophyllide Accumulation in *Arabidopsis*

The de-etiolation of seedlings is a process of greening and chlorophyll synthesis. This transformation of seedlings is realized by the reduction of protochlorophyllide, which is synthesized in the dark. Excessive accumulation of protochlorophyllide is phototoxic to plants, so the accumulation and transformation of protochlorophyllide during the dark-to-light transition are critical for seedling survival. Our Previous studies shown that RAF35-MKK5-MPK6 cascade participates in the photomorphogenesis by inhibiting the accumulation of protochlorophyllide. However, the downstream substrate of this cascade and the regulatory mechanism remain unknown. In this study, we found that GSA1, an enzyme in the chlorophyll synthesis pathway catalyzing the conversion of GSA to ALA, interacts with MPK6 in yeast. MPK6 phosphorylated GSA1 *in vitro*. The content of protochlorophyllide in *raf35*, *mkk5*, *mpk6* and *gsa1* etiolated seedlings significantly increased in compare with that in Col-0. These data suggest RAF35-MKK5-MPK6 cascade negatively regulates the content of protochlorophyllide in seedlings by phosphorylating GSA1, providing important evidences in understanding the regulatory mechanism of chlorophyll synthesis.

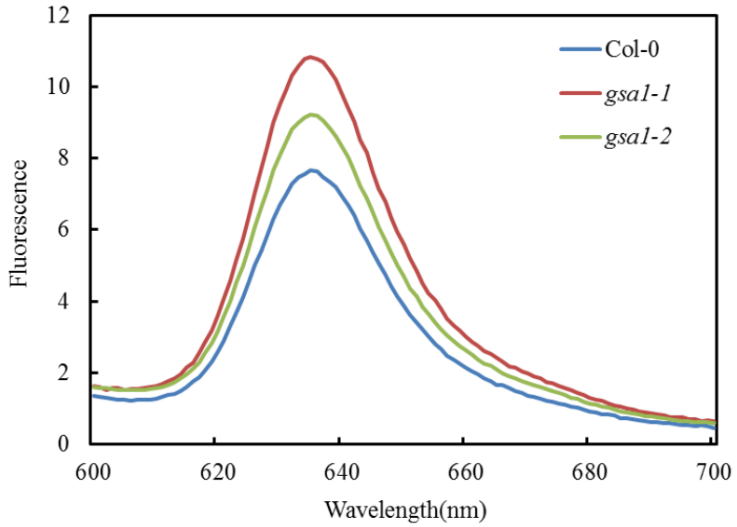


图 2、*gsa1*突变体黄化幼苗中原叶绿素酸酯含量较Col-0明显升高。

Figure 2. The content of protochlorophyllide in *gsa1* etiolated seedlings significantly increased in compare with that in Col-0.

（二） 研究成果

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

Li Y, Liu K, Tong G, Xi C, Liu J, Zhao H, Wang Y, **Ren D**, Han S* (2022) MPK3/MPK6-mediated phosphorylation of ERF72 positively regulates resistance to *Botrytis cinerea* through directly and indirectly activating the transcription of camalexin biosynthesis enzymes. ***J Exp Bot*** 73: 413.

（三） 研究队伍

固定人员：

任东涛（课题组长），李媛。

研究生：

刘骨挺，朱帆，张秀艳，陈晨曦，张子娟，董婷婷，黄昊天，崔立娇，邵瑞华，周漠，吴楚淋，吴霜，尚卿。

苏　震

课题组

苏震，教授。

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

1、KNOX II 转录因子 HOS59 参与调控水稻籽粒大小

Knotted1-like homeobox（KNOX）是一类存在于所有植物中含有同源异形盒结构域的转录因子。植物中有两个具有拮抗作用KNOX蛋白亚家族，分别是具有转录激活能力的KNOX I和具有转录抑制能力的KNOX II。水稻是单子叶模式植物，是世界上最重要的粮食作物之一。在水稻中，KNOX I家族成员的上游调控因子、共同作用因子和下游靶基因已经通过多种方法被鉴定到。然而，目前对于KNOX II家族基因的功能仅有初步了解，其互作蛋白和全基因组水平上的下游靶标基因还知之甚少。随着高通量技术和生物信息学手段的发展和应用，多组学数据的深入分析给我们提供了更开阔的生物学研究视角。

本研究主要以水稻KNOX II成员HOS59（HOMEOBOX ORYZA SATIVA59）为研究对象，首先采用ChIP-seq分析对HOS59的全基因组结合位点和可能的下游靶基因进行了鉴定。对两个重复中出现的9705个下游靶基因使用PlantGSAD（http://systemsbiology.cpolar.cn/PlantGSEAv2/）数据库，进行基因本体论（GO）和农艺性状本体（TO）富集分析，结果表明HOS59可能调控植株形态、籽粒大小等生长发育方面农艺性状与一些生物胁迫和非生物胁迫等抗逆方面农艺性状。接着利用免疫共沉淀结合质谱（IP-MS）检测发现，HOS59与多种蛋白可能发生互作，包括BELL家族蛋白、籽粒大小调控因子（如*OsSPL13*、*OsSPL16*、*OsSPL18*、*SRS5*等）以及一些表观遗传修饰因子（如OsAGO4α和OsAGO4β）。进一步采用CRISPR/Cas9编辑系统和转基因方法分别获得了*hos59*突变体和*HOS59*过表达水稻株系。与野生型相比，*hos59*突变体粒长和颖壳细胞长度增加，并表现为松散株型以及披垂叶性状，而*HOS59*过表达株系籽粒较小，叶片直立，株高降低。qRT-PCR结果显示，*HOS59*基因突变导致*OsSPL13*、*OsSPL18*、*PGL2*等一些籽粒大小相关基因的表达上调。

上述结果表明，HOS59可能负调控下游靶基因，进而负调节颖壳细胞长度、水稻籽粒大小以及株型等。这些发现丰富了对于KNOX Class II家族成员功能的理解，并且填补了该家族调控网络研究的空白。同时，这种系统生物学方法对于研究转录因子的调控功能和分子设计育种提供了新的思路。（Sheng et al., *Plant J*, 2022）

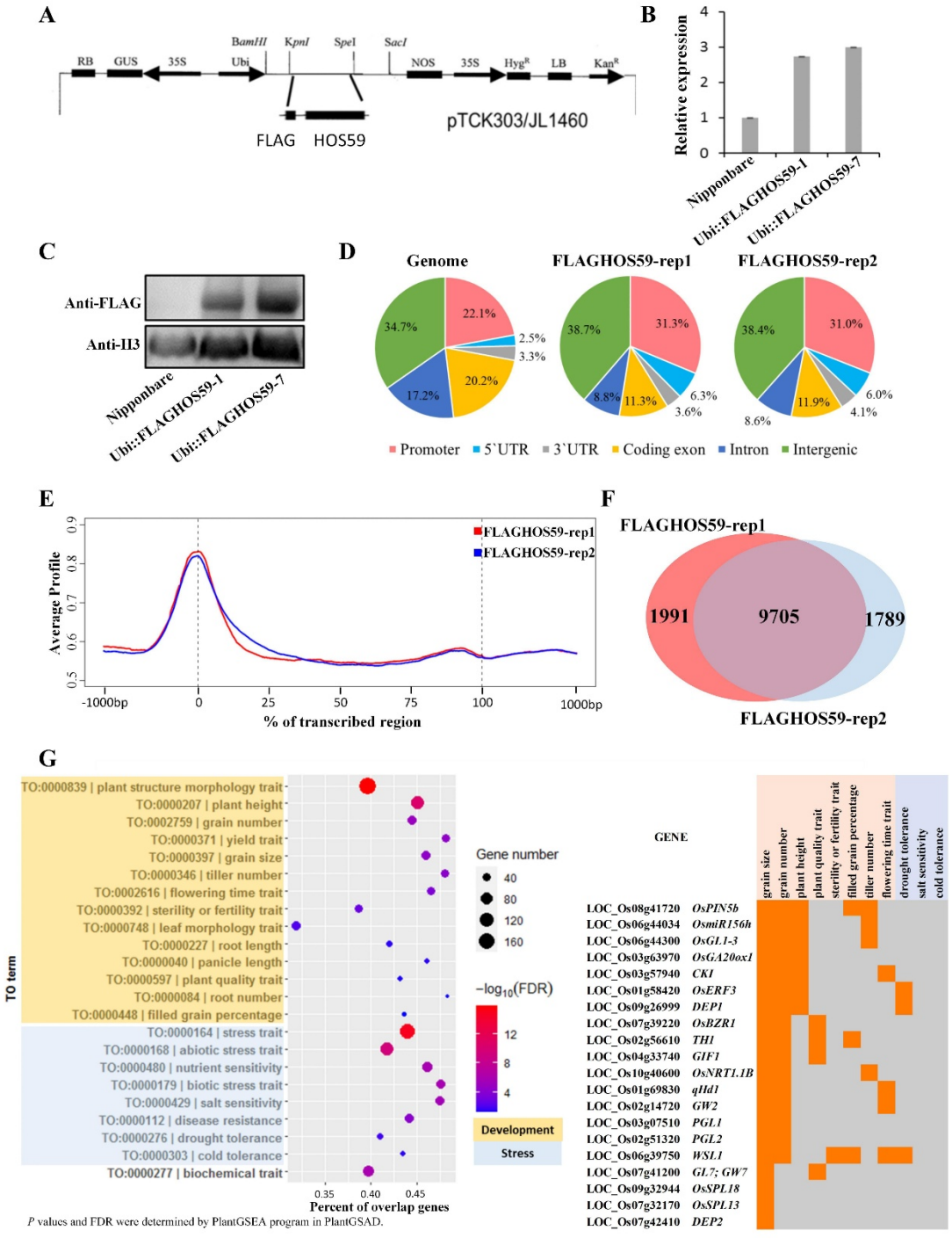


图1、HOS59下游结合基因功能分析。

KNOX II Transcription Factor HOS59 Functions in Regulating Rice Grain Size

Plant Knotted1-like homeobox (KNOX) genes encode homeodomain-containing transcription factors. In rice (*Oryza sativa* L.), little is known about the downstream target genes of KNOX Class II subfamily proteins. Here we generated chromatin immunoprecipitation(ChIP)-sequencing datasets for HOS59, a member of the rice KNOX Class II subfamily, and characterized the genome-wide binding sites of HOS59. We conducted trait ontology (TO) analysis of 9705 identified downstream target genes, and found that multiple TO terms are related to plant structure morphology and stress traits. ChIP–quantitative PCR (qPCR) was conducted to validate some key target genes. Meanwhile, our IP-MS datasets showed that HOS59 was closely associated with BELL family proteins, some grain size regulators (OsSPL13, OsSPL16, OsSPL18, SLG, etc.), and some epigenetic modification factors such as OsAGO4a and OsAGO4b, proteins involved in small interfering RNA-mediated gene silencing. Furthermore, we employed CRISPR/Cas9 editing and transgenic approaches to generate *hos59* mutants and overexpression lines, respectively. Compared with wild-type plants, the *hos59* mutants have longer grains and increased glume cell length, a loose plant architecture, and drooping leaves, while the overexpression lines showed smaller grain size, erect leaves, and lower plant height. The qRT-PCR results showed that mutation of the *HOS59* gene led to upregulation of some grain size-related genes such as *OsSPL13*, *OsSPL18*, and *PGL2*. In summary, our results indicate that HOS59 may be a repressor of the downstream target genes, negatively regulating glume cell length, rice grain size, plant architecture, etc. The identified downstream target genes and possible interaction proteins of HOS59 improve our understanding of the KNOX regulatory networks (Sheng et al., *Plant J*, 2022).

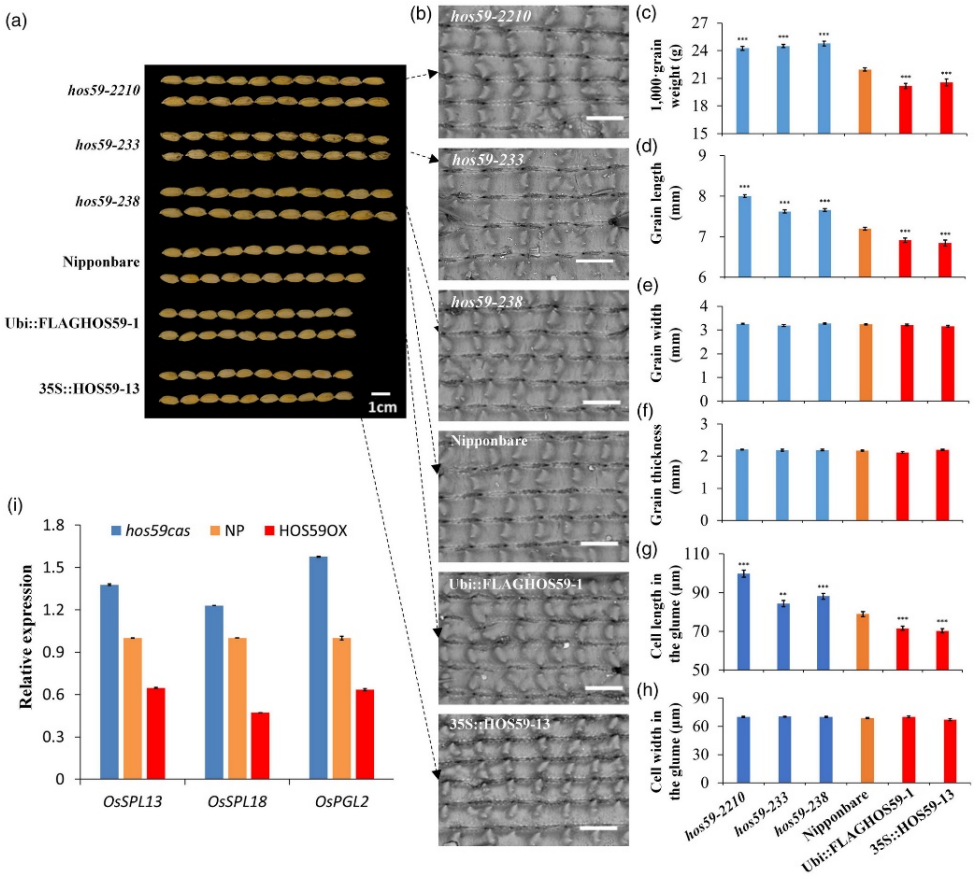


图2、HOS59缺失导致籽粒增长。

2、麦类多维组学数据整合及比较分析平台 WheatCENet

自2017年以来，六倍体小麦及其祖先种的高质量参考基因组相继发布，利用新的策略（例如直系同源基因功能转化、大规模的表达谱数据以及共表达网络的应用）快速预测基因功能并扩大基因注释范围成为当今主要趋势。尽管公共平台已积累了不少小麦及其祖先种的RNA-seq数据，但现有的麦类数据库主要集中在六倍体小麦组学数据，并且主要以提供检索、下载和可视化相关数据为主。然而对于诸如六倍体小麦与其祖先种间的比较分析平台，特别是针对它们多组学数据挖掘和进化研究为主的二级数据库目前还较为缺乏。

本研究整合了来自NCBI的425个小麦及其祖先种（112个六倍体小麦中国春，153个野生二粒小麦，90个乌拉尔图小麦和70个粗山羊草小麦）的RNA-seq数据和一些六倍体小麦中国春的表观基因组数据，构建了包括二倍体、四倍体和六倍体小麦在内的6个共表达网络（4个全局网络和2个条件网络），并建立了一个用于比较六倍体小麦及其祖先种共表达网络的组学数据库平台WheatCENet（http://bioinformatics.cau.edu.cn/WheatCENet），试图阐明六倍体小麦形成过程中两次异源多倍化后在遗传和表观遗传层面的进化特征。WheatCENet既支持6个网络的单基因或多基因搜索（图3A），也支持网络间比较，包括六倍体小麦的全局网络与条件网络间的比较（图3B）、六倍体小麦与其祖先种两两之间的网络比较以及三个不同倍性小麦物种间的网络比较（图3C）。对于单基因的搜索，

可以根据目标基因获得与其共表达的基因集信息；而对于多基因的搜索，既可以获得与目标基因集的共表达的基因集信息，也可以获得目标基因集内部是否存在共表达关系。此外，也可以对目标基因的直系同源基因进行检索，并分析其对应的共表达基因集。对于网络中对应物种的基因集，均支持GSEA分析、GO分析以及motif分析，以发现潜在的基因功能和转录调控区（图3D）。此外，WheatCENet还提供网络中基因集的表达谱信息，及其在染色体上的位置分布信息（图3E）。WheatCENet还提供了个性化的GO分析工具、GSEA分析工具、motif分析工具及其它便捷的小工具（BLAST，不同基因组版本间的ID转换，基因和启动子序列的提取和下载，表达谱信息的提取与可视化），帮助用户多维度研究并理解关键基因功能（Li et al., *Genom Proteom Bioinf*, 2022）。

Wheatcenet: A Database for Comparative Co-Expression Networks Analysis of Allohexaploid Wheat and its Progenitors

Genetic and epigenetic changes after polyploidization events could result in variable gene expression and modified regulatory networks. Here, using large-scale transcriptome data, we constructed co-expression networks for diploid, tetraploid, and hexaploid wheat species, and built a platform for comparing co-expression networks of allohexaploid wheat and its progenitors, named WheatCENet. WheatCENet is a platform for searching and comparing specific functional co-expression networks, as well as identifying the related functions of the genes clustered therein. Functional annotations like pathway, gene family, protein-protein interactions, microRNA (miRNA), and several lines of epigenome data are integrated into this platform, and gene ontology (GO) annotation, gene set enrichment analysis (GSEA), motif identification, and other useful tools are also included. Using WheatCENet, we found that the network of WHEAT ABERRANT PANICLE ORGANIZATION 1 (WAPO1) has more co-expressed genes related to spike development in hexaploid wheat than its progenitors. We also found a novel motif of CCWWWWWWGG (CArG) specifically in the promoter region of WAPO-A1, suggesting that neofunctionalization of the WAPO-A1 gene affects spikelet development in hexaploid wheat. WheatCENet is useful for investigating co-expression networks and conducting other analyses, and thus facilitates comparative and functional genomic studies in wheat. WheatCENet is freely available at http://bioinformatics.cpolar.cn/ WheatCENet and http://bioinformatics.cau.edu.cn/WheatCENet (Li et al., *Genom Proteom Bioinf*, 2022).

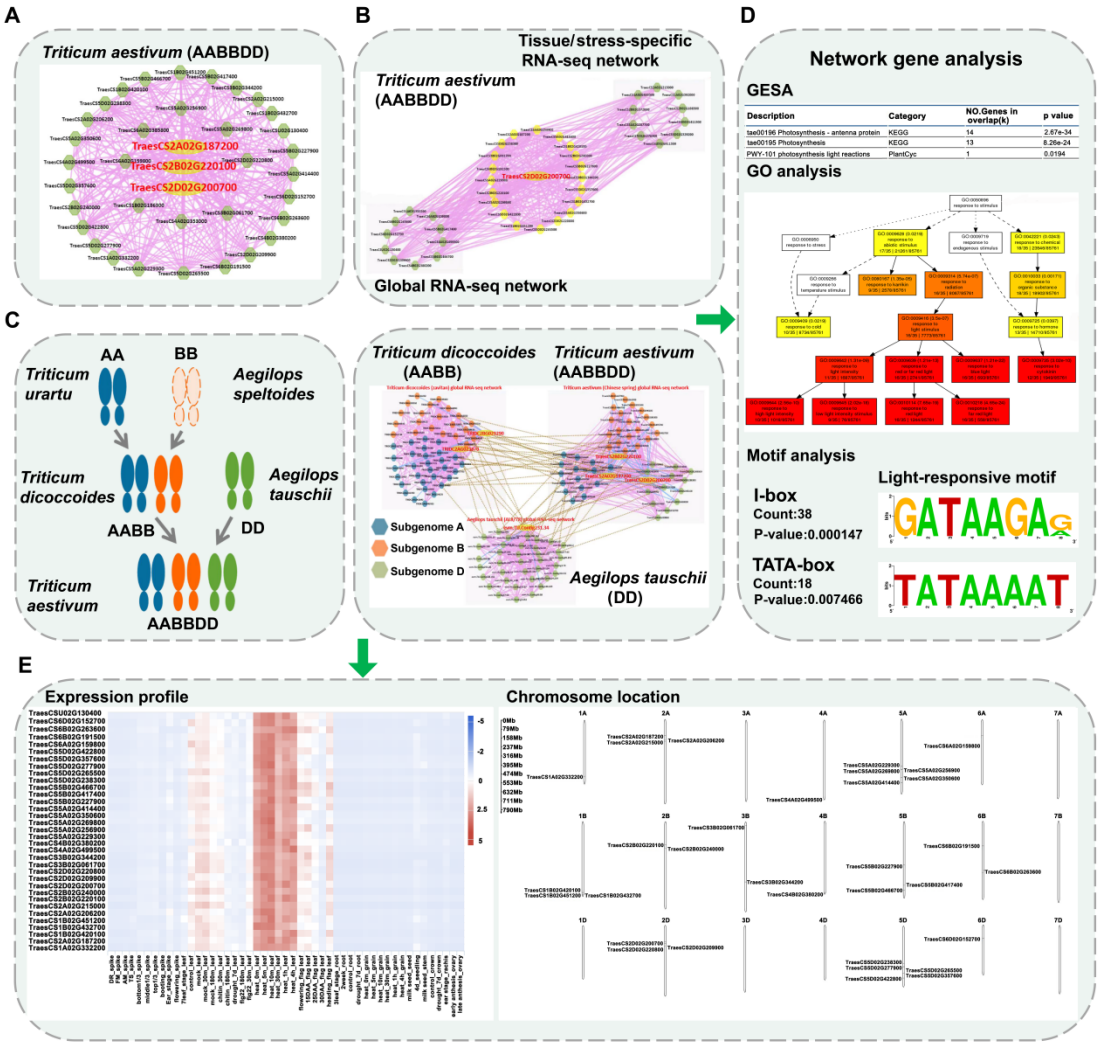


图3、WheatCENet中的网络分析。

（二） 研究成果

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

1. Sheng M, Ma X, Wang J, Xue T, Li Z, Cao Y, Yu X, Zhang X, Wang Y, Xu W, **Su Z*** (2022) KNOX II transcription factor HOS59 functions in regulating rice grain size. ***Plant J*** 110: 863-880.
2. Sheng M[#], Da L[#], Song Q, Liu Y, Zhang X, Liu F, Xu W, **Su Z*** (2022) Systems biology-based analysis indicates that *PHO1;H10* positively modulates high light-induced anthocyanin biosynthesis in *Arabidopsis* leaves. ***Genomics*** 114: 110363.
3. Li Z, Hu Y, Ma X, Da L, She J, Liu Y, Yi X, Cao Y, Xu W, Jiao Y*, **Su Z*** (2022) WheatCENet: a database for comparative co-expression networks analysis of allohexaploid wheat and its progenitors. ***Genom Proteom Bioinf*** doi: 10.1016/j.gpb.2022.04.007.

4. Yang J, Yan H, Liu Y, Da L, Xiao Q, Xu W*, **Su Z*** (2022) GURFAP: a platform for gene function analysis in *Glycyrrhiza uralensis*. ***Front Genet*** 13: 823966.
5. Jiang L#, Liu Y#, Wen Z#, Yang Y#, Singer S, Bennett D, Xu W, **Su Z**, Yu Z, Cohn J, Luo X, Liu Z, Chae H, Que Q, Liu Z* (2022) CW198 acts as a genetic insulator to block enhancer-promoter interaction in plants. ***Transgenic Res*** doi: 10.1007/s11248-022-00326-6.

获批专利：

拟南芥 PHO1;H10 蛋白及其编码基因在调控植物叶片花青素合成中的应用。申请人：**苏震**，徐文英，达玲玲，宋倩，刘凤霞，张群莲；专利号：ZL201911323001.9；授权日期：2022 年 04 月 26 日。

（三） 研究队伍

固定人员：

苏震（课题组长）。

研究生：

盛铭浩（2022 年 6 月毕业），李中秋（2022 年 6 月毕业），曹亚欣，于新月，薛天玺，张心怡，金虹，梁亚伟。

秦　峰

课题组

秦峰，教授。

研究方向：玉米响应干旱胁迫的基因资源挖掘与分子功能解析。

（一） 研究进展

ZmSRO1d 调控玉米平衡生长与干旱胁迫应答中的机制解析

玉米是我国种植面积最大、产量最高的作物，由于其植株高大，需水量多，对于干旱非常敏感，然而我国玉米主要栽培区多位于干旱半干旱地区，每年因旱灾造成玉米大幅减产，带来巨大的经济损失，严重威胁着我国的粮食安全。尤其伴随着全球气候变化，干旱的发生频率也在不断升高，因此，挖掘玉米抗旱性相关的基因资源，解析其功能并加以利用具有非常重要的研究价值和现实意义。自然选择以物种的后代繁衍为目标，环境适应性强的优异的基因型更多的被选择。但作物育种主要以追求产量为目标，人为选择产量性状表现优异的基因型。因此，在现代玉米育种过程中，玉米的产量被大幅提高，然而玉米抗旱性却显著下降。这也证实作物产量性状和抗逆性状之间存在平衡关系。挖掘调控玉米抗旱性与产量之间平衡相关的遗传位点并解析其遗传与分子作用机制，探究作物的抗旱性与产量之间的平衡关系，有助于突破高抗高产作物育种面临的瓶颈问题。

通过全基因组关联分析，发现位于玉米第9染色体的*ZmSRO1d*基因上的遗传变异与玉米苗期抗旱性极显著相关，该基因中3个显著的非同义突变（SNP131、SNP134、和SNP488）可以将*ZmSRO1d*分为*ZmSRO1d-S*（干旱敏感）和*ZmSRO1d-R*（抗旱）两种单倍体型。抗旱优异等位基因型蛋白ZmSRO1d-R能与Zm14-3-3.1互作并定位到质膜对ZmRBOHC进行ADP核糖基化修饰，导致保卫细胞内的ROS产生增加，从而促进气孔的闭合，增强玉米的抗旱性。通过对转基因材料的苗期存活率和产量进行分析，发现*ZmSRO1d*两种单体型的过表达玉米均可以提高玉米苗期的抗旱性，其中*ZmSRO1d-R*的抗旱性更为明显，可以显著提高干旱胁迫下玉米的产量，但是会减少玉米在正常水分条件下的产量，而*ZmSRO1d-S*基因型不影响玉米正常水分条件下的产量。进一步对基因型频率进行分析，发现ZmSRO1d-S基因型在玉米驯化和现代育种中存在明显的选择，可能由于*ZmSRO1d-R*基因型影响正常水分条件下的产量，而发生了人工选择性清除。*ZmSRO1d*自然变异的发现及其功能解析，为以后玉米高产、稳产的新品种培育提供了新的认识和思考。该研究成果于2022年10月在《*Molecular Plant*》上以长文形式发表（Gao et al., *Mol Plant*, 2022）。

Genetic Dissection of Zmsro1d Modulating the Trade-Off Between Drought Resistance and Yield in Maize

Maize is a major crop with the largest planting area and the highest yield in China. Miaze plant is very sensitive to drought due to its large plant size and high water requirement. However, most of the main cultivation areas of maize are located in arid and semi-arid areas. With the global climate change, drought occurs more frequently. To mine the gene resources related to drought resistance in maize and dissect their functions to further breeding application are of great important. Natural selection aims at the progeny of a species, therefore more favorable genotypes are selected for environmental fitness. However, crop breeding mainly aims at yield and artificially selects the genotypes with excellent yield traits. Thus, in the process of breeding, the yield of maize is greatly increased, while the drought resistance of corn is significantly decreased. This also reflects the trade-offs between yield traits and stress resistance traits. Exploring the genetic loci related to regulating the balance between drought resistance and yield of maize, and revealing the underlying genetic and molecular mechanisms will help to break through the bottleneck scientific problem of high resistance and high yield crop breeding.

Through genome-wide association studies, we found that the genetic variation of *ZmSRO1d* gene located on chromosome 9 of maize genome was significantly correlated with drought resistance at seedling stage of maize. According to the three significant non-synonymous mutations in this gene (SNP131, SNP134, and SNP488), different maize germplasms could be classified into two haploid types: *ZmSRO1d-S* (drought sensitive) and *ZmSRO1d-R* (drought resistant). The favorable drought resistance allele *ZmSRO1d-R* can interact with Zm14-3-3.1 and locate to the plasma membrane for ADP riboylation modification of ZmRBOHC, resulting in increased production of ROS in guard cells, thus promoting stomatal closure and enhancing drought resistance of maize. By analyzing the survival rate and yields of transgenic materials, it was found that both of these two haplotypes overexpression maize of *ZmSRO1d* could both improve the drought resistance of maize at the seedling stage, and the drought resistance of *ZmSRO1d-R* was more obvious, which could significantly improve the yield of maize under drought stress, but reduce the yield of maize under normal moisture conditions. While, *ZmSRO1d-S* genotype did not affect the yield of maize under normal water condition. Further analysis of genotype frequency showed that *ZmSRO1d-S* genotype had been selection in maize domestication and modern breeding, which may be due to the effect of ZmSRO1d-R genotype on the yield under normal water conditions, and the artificial selective clearance occurred. The identification and molecular study of natural variations of *ZmSRO1d* provided new understanding for maize breeding with high drought resistance and stable of high yield in the future.

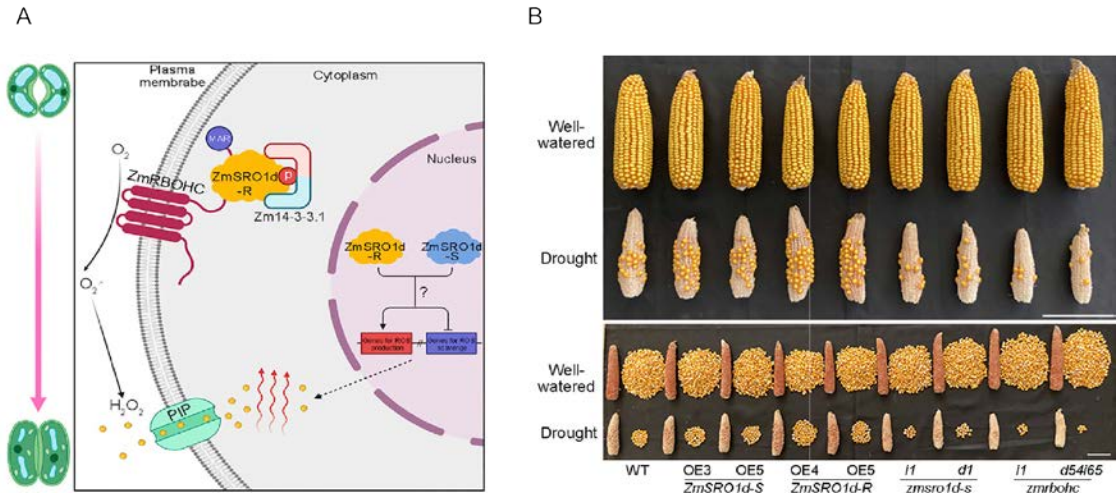


图1、ZmSOR1d调控玉米响应干旱胁迫与产量之间的平衡。A. ZmSOR1d介导气孔闭合增强玉米抗旱性的模式图；B. *ZmSOR1d*过表达与突变体材料在正常浇水和干旱条件下的产量性状。

Figure 1. ZmSOR1d modulates the trade-off between drought resistance and yield in maize. A. The working model for ZmSOR1d-mediated drought-induced stomatal clourse signaling to enhance drought resistance. B. The yield phenotypes of overexpression and knockout materials of *ZmSOR1d* under well-watered and drought conditions.

（二） 研究成果

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

Gao H, Cui J, Liu S, Lian Y, Bai Y, Zhu T, Wu H, Wang Y, Yang S, Li X, Zhuang J, Chen L, Gong Z, **Qin F*** (2022) Natural variations of ZmSRO1d modulate the trade-off between drought resistance and yield by affecting ZmRBOHC-mediated stomatal ROS production in maize. ***Mol Plant*** 15: 1558-1574.

（三） 研究队伍

固定人员：

秦峰（课题组长），刘升学，杨志蕊。

博士后：

杨世平，田甜，王妍妍，赵军。

研究生：

王琛，米悦，刘燕，王书会，朱腾飞，练永燕，王懿杰，韩玉芳，朱朝晖，刘玉，吴昊浩，白云婷，崔俊俊，黄琴，赵博琛，洪静怡，秦凝，付晓萌，马超，贺佳凡，叶树青，王梦圆，王子阳。

毛同林 课题组

毛同林，教授。

研究方向：细胞骨架参与植物响应环境信号的分子机制。

（一） 研究进展

1、OST1–SPR1 元件调控 ABA 诱导的微管解聚和气孔关闭过程

气孔是植物叶片及茎表皮上由一对保卫细胞组成的小孔，是植物与外界进行气体交换和水分蒸腾的通道，对植物响应外界环境至关重要。在植物受到干旱胁迫时，激素脱落酸（abscisic acid, ABA）诱导气孔关闭，避免水分的过多损失。在ABA诱导的气孔关闭过程中，微管骨架迅速解聚。但是ABA信号是如何诱导微管骨架解聚的具体机制并不清楚。微管结合蛋白是调控微管组织排列和动态变化的关键因子，目前为止，ABA信号通路与微管结合蛋白之间的直接调控关系仍然未知。我们通过细胞生物学、生物化学和分子遗传学等手段发现微管结合蛋白SPIRAL1（SPR1）可以被ABA信号通路中的核心组分OPEN STOMATA 1（OST1）磷酸化，直接参与ABA诱导的微管解聚以及气孔关闭过程。研究结果表明，突变体*spr1-6*在ABA处理下气孔闭合程度和保卫细胞中微管解聚程度均显著低于野生型，模拟持续磷酸化形式的SPR1可以回补该表型，而模拟非磷酸化形式的SPR1则不能，说明SPR1是ABA诱导微管解聚和气孔关闭的正调控因子，且此功能依赖于OST1对SPR1的磷酸化。进一步的细胞学分析表明，磷酸化形式SPR1的细胞学定位发生改变，从微管上解离，并促进微管解聚（图 1）。该研究建立了微管结合蛋白SPR1与ABA信号通路中的关键激酶OST1之间的直接联系，揭示了SPR1调控ABA诱导气孔关闭的分子功能，为进一步解析复杂而精细的气孔运动调控网络提供了重要的细胞学依据（Wang et al., *Plant Cell*, 2022）。

The OPEN STOMATA1-SPIRAL1 Module Regulates Microtubule Stability during Abscisic Acid-induced Stomatal Closure in *Arabidopsis*

Drought stress triggers abscisic acid (ABA) signaling in guard cells and induces stomatal closure to prevent water loss in land plants. Stomatal movement is accompanied by reorganization of the cytoskeleton. Cortical microtubules disassemble in response to ABA, which is required for stomatal closure. However, how ABA signaling regulates microtubule disassembly is unclear, and the microtubule-associated proteins (MAPs) involved in this process remain to be identified. In this study, we show that OPEN STOMATA 1 (OST1), a central component in ABA signaling, mediates

microtubule disassembly during ABA-induced stomatal closure in *Arabidopsis thaliana*. We identified the MAP SPIRAL1 (SPR1) as the substrate of OST1. OST1 interacts with and phosphorylates SPR1 at Ser6, which promotes the disassociation of SPR1 from microtubules and facilitates microtubule disassembly. Compared with the wild type, the *spr1* mutant exhibited significantly greater water loss and reduced ABA responses, including stomatal closure and microtubule disassembly in guard cells. These phenotypes were restored by introducing the phosphorylated active form of SPR1. Our findings demonstrate that SPR1 positively regulates microtubule disassembly during ABA-induced stomatal closure, which depends on OST1-mediated phosphorylation. These findings reveal a specific connection between a core component of ABA signaling and MAPs (Wang et al., *Plant Cell*, 2022).

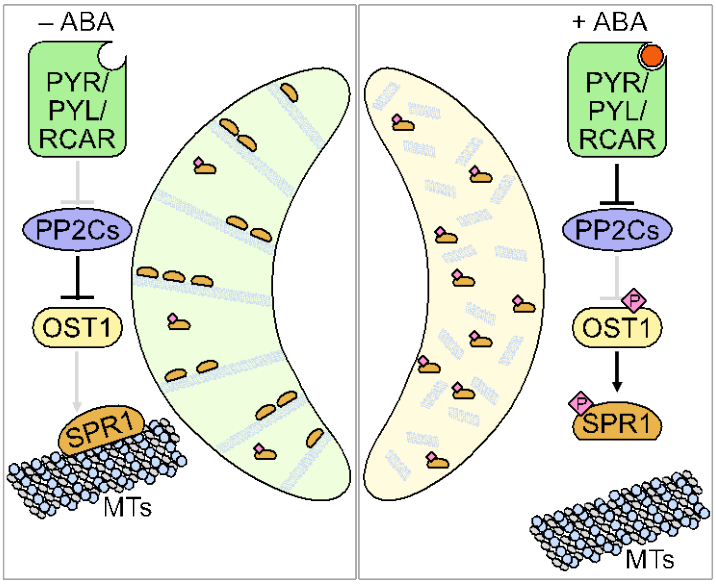


图1、OST1-SPR1调控ABA诱导微管解聚以及气孔关闭的分子模型。

Figure 1. A working model for OST1-SPR1 regulating microtubule disassembly and stomatal closure in response to ABA.

2、光信号通路转录因子 HY5 通过微管骨架参与调控侧根发生的分子机制

侧根是双子叶植物根系结构的重要组成部分，合适的侧根数目有利于提高根系结构的可塑性，以便植物更好的吸收水分和养分以及适应多变的土壤环境。侧根起始是决定侧根发育的基础。在拟南芥侧根起始时，质微管重组对侧根建成细胞的不对称径向扩张是必要的。我们发现微管结合蛋白*tpxl5*突变体的侧根密度减少并且滞留在阶段Ⅰ的侧根原基较多。细胞学定位和功能分析发现，TPXL5是一个微管结合蛋白并稳定微管。观察侧根起始时第一次不对称分裂后侧根建成细胞的径向扩张和微管组织排列发现，突变体*tpxl5*建成细胞的中心区域和边缘区域的径向扩张明显增加，且边缘区域微管组织排列更加紊乱。进一步研究发现，光信号通路的重要转录因子HY5直接结合*TPXL5*的启动

子区并抑制*TPXL5*的表达。突变体*hy5*的侧根密度增加并且滞留在阶段Ⅰ的侧根原基较少；建成细胞边缘区域的径向扩张减少并且微管组织呈现更加垂直于细胞长轴的排列。在*tpxl5 hy5*双突变体中，与*hy5*突变体相比，侧根密度减少并且滞留在阶段Ⅰ的侧根原基增加。该研究为揭示周质微管重组对侧根起始的必要性提供了重要遗传学证据；阐明了在侧根起始过程中，HY5-TPXL5调控元件介导的微管重组和细胞重塑的新机制（图2），为提高植物根系结构可塑性提供了新思路（Qian et al., *Plant Cell*, 2022）。

HY5 Inhibits Lateral Root Initiation in *Arabidopsis* through Negative Regulation of the Microtubule-Stabilizing Protein TPXL5

Tight control of lateral root (LR) initiation is vital for root system architecture and function. Regulation of cortical microtubule reorganization is involved in the asymmetric radial expansion of founder cells during LR initiation in *Arabidopsis* (*Arabidopsis thaliana*). However, critical genetic evidence on the role of microtubules in LR initiation is lacking and the mechanisms underlying this regulation are poorly understood. Here, we found that the previously uncharacterized microtubule-stabilizing protein TPXL5 participates in LR initiation, which is finely regulated by the transcription factor ELONGATED HYPOCOTYL5 (HY5). In *tpxl5* mutants, LR density was decreased and more LR primordia (LRPs) remained in stage I, indicating delayed LR initiation. In particular, the cell width in the peripheral domain of LR founder cells after the first asymmetric cell division was larger in *tpxl5* mutants than in the wild type. Consistently, ordered transverse cortical microtubule arrays were not well generated in *tpxl5* mutants. In addition, HY5 directly targeted the promoter of *TPXL5* and downregulated *TPXL5* expression. The *hy5* mutant exhibited higher LR density and fewer stage I LRPs, indicating accelerated LR initiation. Such phenotypes were partially suppressed by *TPXL5* knockout. Taken together, our data provide genetic evidence supporting the notion that cortical microtubules are essential for LR initiation and unravel a molecular mechanism underlying HY5 regulation of TPXL5-mediated microtubule reorganization and cell remodeling during LR initiation (Qian et al., *Plant Cell*, 2022).

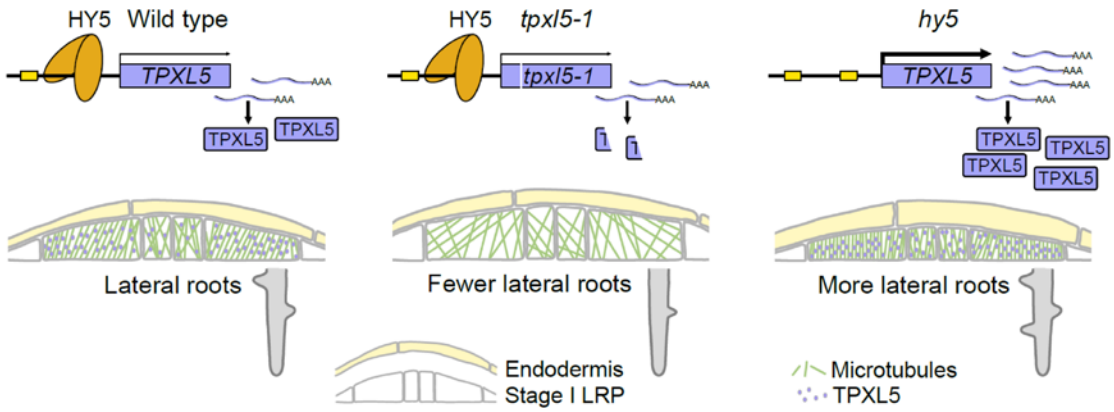


图2、HY5-TPXL5调控侧根发生的分子模型。

Figure 2. A working model for the function of TPXL5 during HY5-mediated LR initiation.

（二） 研究成果

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

1. Wang P#, Qi S#, Wang X, Dou L, Jia M, **Mao T**, Guo Y*, and **Wang X*** (2022) The OPEN STOMATA1–SPIRAL1 module regulates microtubule stability during abscisic acid-induced stomatal closure *in Arabidopsis*. ***Plant Cell*** doi: 10.1093/plcell/koac307.
2. Qian Y#, Wang X#, **Liu Y**, **Wang X***, **Mao T*** (2022) HY5 inhibits lateral root initiation in *Arabidopsis* through negative regulation of the microtubule-stabilizing protein TPXL5. ***Plant Cell*** Accepted.

（三） 研究队伍

固定人员：

毛同林（课题组长），王向锋。

研究生：

钱艳敏，王攀，王若茜，耿鑫，秦静，齐思佳，张欣媛，赵晓菁，李保磊，宋卫娜，王盼盼，袁冰，邸宏超。

李召虎

课题组

李召虎，教授。

研究方向：（1）作物抗逆高产调控机理与化控技术；（2）植物生长调节剂创制与激素调控机制。

（一） 研究进展

1、ABA 诱导 NO 合成调控棉花应答干旱胁迫的分子机制

ABA 诱导 NO 积累触发气孔关闭，NO-ABA 互作的关键节点目前亟待揭示。OST1 是 ABA 信号途径中的核心蛋白激酶，为研究 GhOST1 对 NO 合成的调控作用，利用酵母双杂筛选获得互作蛋白激酶 GhNAGK，该激酶是 NO 合成前体物质精氨酸合成的限速酶。前期的研究结果表明 VIGS 沉默 *GhOST1* 或 *GhNAGK* 的棉花幼苗对干旱胁迫敏感。进一步研究明确了 GhNAGK 与 GhOST1 在棉花原生质体中互作。体外磷酸化试验表明 GhOST1 可磷酸化修饰 GhNAGK，质谱鉴定磷酸化位点结果表明 GhOST1 主要磷酸化 GhNAGK 的 Thr163 与 Thr167 位点，且点突显著抑制了 GhNAGK 的激酶活性。通过 NO 特异性荧光探针成像分析，可见 VIGS 沉默 *GhOST1* 或 *GhNAGK* 均能显著抑制 ABA 诱导的气孔保卫细胞中 NO 积累和气孔关闭，外源添加 L-精氨酸和 NO 供体 SNP 可恢复气孔表型。同时，外源处理精氨酸和 NO 均能提高棉花幼苗的抗旱性，显著提高干旱胁迫下叶片的相对含水量。上述研究结果表明 GhOST1 可通过磷酸化激活 GhNAGK 诱导干旱胁迫下 NO 在保卫细胞中的富集，进而调节气孔开闭应答干旱胁迫。

Molecular Mechanism of ABA Induces NO Biosynthesis Regulating Drought Stress Response in Cotton

ABA-induced NO accumulation is necessary to trigger stomatal closure, However the key nodes of NO-ABA interaction is still uncover. The protein kinase OST1 is the core member of ABA signal pathway. In order to explore NO related components interacting with GhOST1, yeast two-hybrid screening was performed and protein kinase GhNAGK, the rate-limiting enzyme of arginine synthesis which is the precursor of NO synthesis, was identified. *VIGS-GhOST1* or *VIGS-GhNAGK* enhanced cotton seedling sensitivity to drought stress. We further confirmed that GhOST1 and GhNAGK interactes in the cotton protoplast. In vitro phosphorylation assay showed that GhOST1 could phosphorylate GhNAGK. Also, the phosphorylation key sites Thr163 and Thr167 were identified by LC-MS. When mutate these two sites, The GhNAGK kinase activity was

signaificantly conpromised. Furthermore, *VIGS-GhOST1* or *VIGS-GhNAGK* could significantly inhibit ABA-induced NO accumulation in stomatal by NO specific fluorescence probe imaging analysis and also the stomata close; however, exogenous application of arginine and NO could recover the stomata close phenotype and improve the drought resistance of cotton seedlings. Thus, the results indicated that GhOST1 could regulate NO accumulation in stomata by phosphorylation of GhNAGK, thus regulating stomatal closure in response to drought stress.

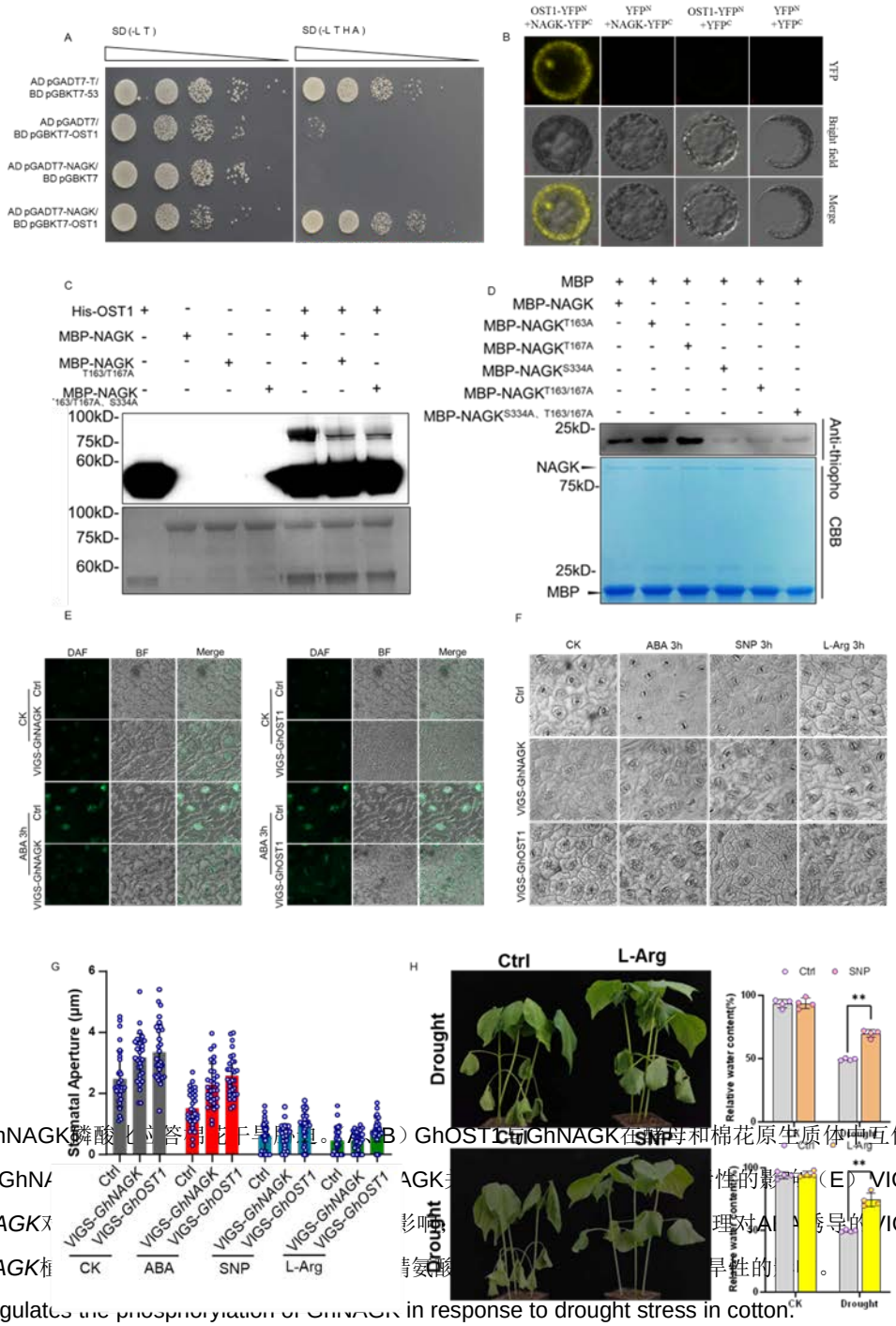


图1、GhOST1调控GhNAGK磷酸化过程参与干旱响应。（A、B）GhOST1与GhNAGK在酵母和棉花原生质体中互作；（C）GhOST1磷酸化GhNAGK关键位点分析；（D）GhNAGK关键位点磷酸化对其激酶活性的影响；（E）VIGS沉默*GhOST1*或*GhNAGK*对ABA诱导的气孔关闭的影响；（F）外源精氨酸处理对ABA诱导的VIGS沉默*GhOST1*或*GhNAGK*植株气孔关闭的恢复；（G）外源精氨酸处理对VIGS沉默*GhOST1*或*GhNAGK*植株干旱性的影响。

Figure 1. GhOST1 regulates the phosphorylation of GhNAGK in response to drought stress in cotton.

(A, B) Analysis of protein interaction between GhOST1 and GhNAGK in yeast and cotton protoplast; (C) Analysis of phosphorylation key site of GhNAGK by GhOST1; (D) The effect of phosphorylation sites mutation on GhNAGK kinase activity; (E) Effects of *VIGS-GhOST1* or *VIGS-GhNAGK* on NO accumulation in stomatal induced

by ABA; (F, G) Effects of arginine and NO donor SNP on stomatal closure induced by ABA; (H, I) Effects of arginine and NO donor SNP on water loss and drought resistance in cotton seedlings.

2、Mn_3O_4 纳米拟酶诱导 Ca^{2+}信号增强棉花萌发期耐旱机制

Mn_3O_4 纳米颗粒是一种新开发的环境友好型纳米拟酶（Nanozyme），其表面 Mn^{2+}与 Mn^{3+}的比例大约为 1:2，具有清除活性氧（ROS，reactive oxygen species）的能力。我们前期的研究发现 Mn_3O_4 纳米拟酶缓解了干旱胁迫对棉花幼苗生长的抑制作用。进一步研究发现 Mn_3O_4 纳米拟酶可促进 PEG 胁迫下棉花萌发期下胚轴和根系的伸长生长，清除 PEG 胁迫在棉花根系诱导的过量 ROS。钙离子（Ca^{2+}）作为第二信使在植物响应不同逆境胁迫中起重要作用，当植物细胞受到胁迫刺激后，胞质中的 Ca^{2+}浓度迅速增加，引发 Ca^{2+}信号。ROS 与 Ca^{2+} 通过“ROS-Ca^{2+}中心”相互调控。本研究发现 Mn_3O_4 纳米拟酶增加了干旱胁迫下棉花根尖 *GhCNGCs* 的表达量。利用非损伤离子微测技术发现 Mn_3O_4 纳米拟酶增强了瞬时 PEG 处理条件下棉花根部的 Ca^{2+}内流。同时，检测转水母荧光蛋白基因的棉花幼苗中钙信号的动态变化规律，发现 PEG 处理可诱导钙信号的快速响应，而 Mn_3O_4 纳米拟酶浸种处理不仅加快了钙信号的响应速度还增强了钙信号应答。活性氧清除剂 DMTU 处理可部分抑制 PEG 胁迫下 Mn_3O_4 纳米拟酶诱导的 Ca^{2+}信号。上述研究结果初步表明 Mn_3O_4 纳米拟酶可通过诱导 Ca^{2+}信号增强棉花耐旱性。

Mechanisms of Mn_3O_4 Nanozymes Regulating Ca^{2+} Signal to Improve Drought Tolerance in Cotton

Mn_3O_4 nanoparticles are a newly developed environmentally friendly nanozyme. The ratio of Mn^{2+} to Mn^{3+} on the surface of Mn_3O_4 nanoparticles is about 1:2, which has the ability to remove reactive oxygen species (ROS). Our previous study found that the Mn_3O_4 nanozymes alleviated the inhibition of drought stress on the growth of cotton seedling. Further studies showed that the Mn_3O_4 nanozymes could promote hypocotyl and root growth, and remove the excessive ROS accumulated in the cotton root under drought stress. As a second messenger, calcium ion (Ca^{2+}) plays an important role in the response of plants to different stresses. When plant cells are stimulated by stresses, the concentration of Ca^{2+} in the cytoplasm increases rapidly, triggering Ca^{2+} signals. Also, ROS and Ca^{2+} interacts with each other through the "ROS-Ca2+ center" under stress condition. Mn_3O_4 nanozymes increased the expression of *GhCNGCs* in cotton root tips under drought stress. Meanwhile, it was found that Mn_3O_4 nanozymes increase Ca^{2+} influx upon transient PEG treatment in cotton roots by non-invasive Micro-test Technology (NMT). The dynamic changes of calcium signals in Aequorin protein transgenic cotton seedlings upon stress were detected, and the results showed that Mn_3O_4 nanozymes enhanced PEG induced Ca^{2+} signal in cotton seedling, which can be partially inhibited by the ROS scavenger DMTU. Together, the results preliminarily indicated that Mn_3O_4 nanozymes could promote Ca^{2+} signal to improve drought tolerance in cotton.

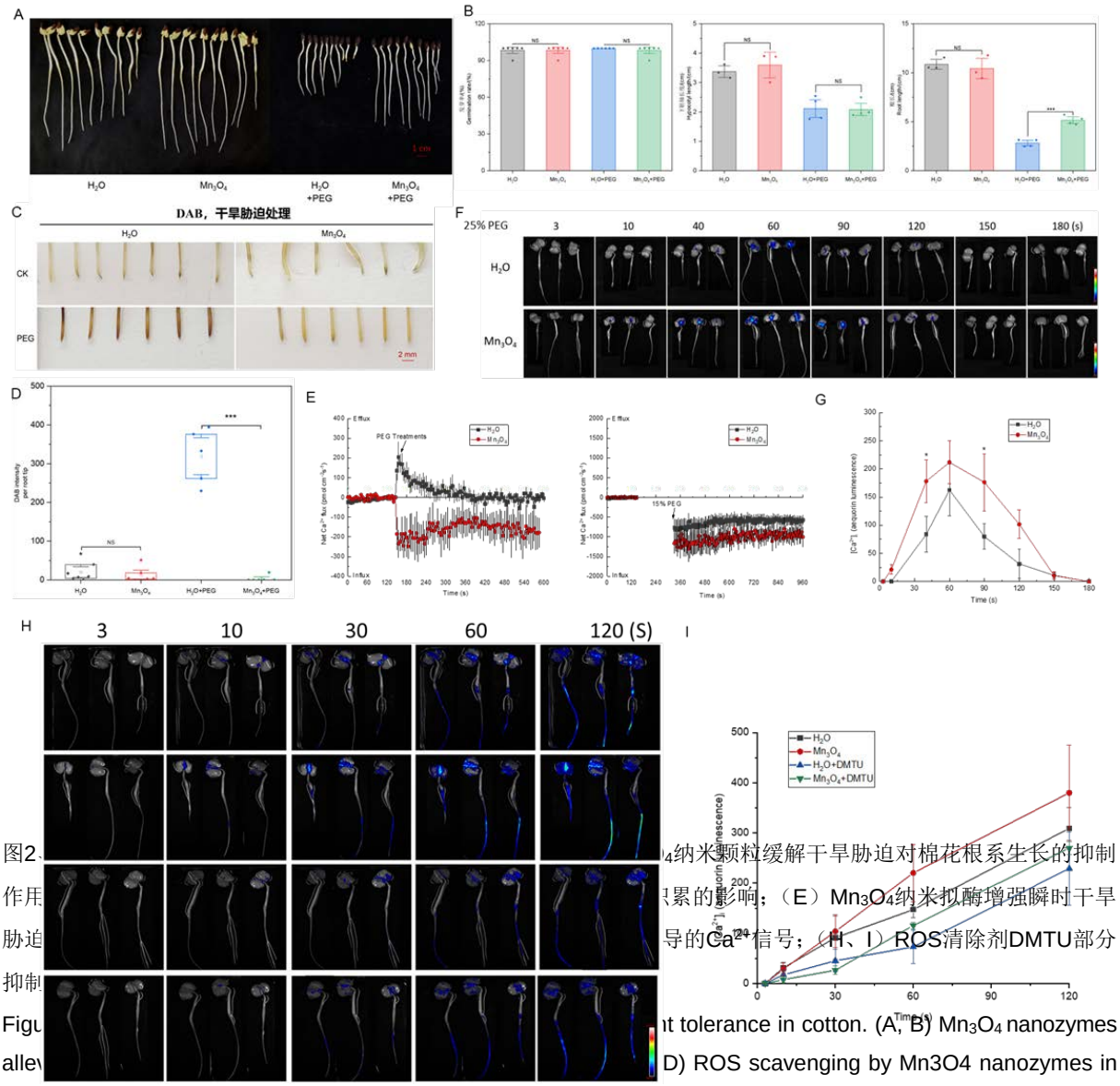


图2、Mn_3O_4纳米颗粒缓解干旱胁迫对棉花根系生长的抑制作用[illegible]累的影响；（E）Mn_3O_4纳米拟酶增强瞬时干旱胁迫[illegible]导的Ca^{2+}信号；（H、I）ROS清除剂DMTU部分抑制[illegible]

Figu[illegible]t tolerance in cotton. (A, B) Mn_3O_4 nanozymes alle[illegible] D) ROS scavenging by Mn3O4 nanozymes in cotton seedling roots under drought stress; (E) Mn_3O_4 nanozymes regulates Ca^{2+} influx upon transient PEG treatment; (F, G) Mn_3O_4 nanozymes enhances PEG induced Ca^{2+} accumulation in cotton seedlings; (H, I) ROS scavenger DMTU partially inhibits Mn_3O_4 nanozymes induced Ca^{2+} accumulation under PEG stress.

3、氮素稳定剂对不同生态区域玉米栽培体系氧化亚氮排放的调控及其微生物响应机制

氮肥过量施用会引发农田氧化亚氮（N_2O）排放激增，N_2O 作为一种强效温室气体会对全球气候变化、生态环境、人类健康产生一系列负面影响。氮素稳定剂（硝化抑制剂，NI；脲酶抑制剂，UI；硝化抑制剂+脲酶抑制剂，UN）是保证玉米绿色栽培体系的潜在工具，但由于气候和土壤条件的差异，氮稳定剂的应用效率在大区域尺度上存在巨大变异。通过两年连续的多点原位田间试验，发现氮稳定剂能够抑制我国玉米农田 1.3–93.9%的 N_2O 排放，同时显著降低产量尺度 N_2O 排放，其中 NI 和 UN 对 N_2O 排放和产量尺度 N_2O 排放的抑制效果较高（A）。通过整个生育期的持续监测发现，氮素稳定剂的持效期是决定其抑制效率的重要因素，随机森林和相关性分析证明，土壤 pH，

空隙含水量，速效磷和土壤质地与氮素稳定剂抑制 N_2O 排放的效率显著相关（B）。同时，通过室内培养试验进一步验证了氮素稳定剂对 N_2O 排放抑制效率的变异主要是由于土壤类型的变化引起（C、D）。通过原位土壤的宏基因组学发现，NI 能够显著改善土壤微生物群落和功能的多样性。不同生态区域玉米田土壤中氮循环相关功能基因对 NI 的响应存在差异，其中仅有羟胺氧化酶基因（*hao*）丰度随氮肥投入显著增加，随 NI 添加显著降低（E）。随机深林和相关性分析进一步验证，*hao* 和携带 *hao* 基因的 *Nitrosospira* 菌属与 NI 的效率呈现显著的正相关关系，进一步说明 *hao* 基因和携带相关基因的菌属对于 NI 抑制 N_2O 排放效率表现出显著的重要性（F）。综上，NI 是大区域尺度上抑制 N_2O 排放的有效工具，而关键环境因子和微生物的变化是决定 NI 效率变化的主要预测因子。

Regulation of Nitrogen Stabilizers on N_2O Emission and Its Microbial Response Mechanism in Maize Cultivation System Across Different Ecological Regions

Over-nitrogen (N) fertilization resulting in huge nitrous oxide (N_2O) emission, and N_2O as a powerful greenhouse gas have led to substantial threats to climatic change, ecological environment, and human health. N stabilizers (i.e., nitrification inhibitor, NI, urease inhibitor, UI, and urease inhibitor + nitrification inhibitor, UN) as the potential tool for green production of maize system, while the efficiency of N stabilizers showed the huge variation across large scale ecological region. Through two-year of consecutive in-situ multiple-field experiment, N stabilizers reduced N_2O emissions by 1.3–93.9% across the multiple-field experiment, and also significantly decreased yield-scale N_2O emissions (YSNEs), wherein NI and UN exhibited higher efficiency on N_2O and YSNEs mitigation (A) Through continuous monitoring of whole maize growth period, the duration of N stabilizers was the key factors for efficiency of N stabilizers. The random forest (RF) and correlation analyses indicated that soil pH, water-filled pore space, available phosphorus, and texture showed significantly correlated with efficiency of N stabilizers on N_2O mitigation (B) Similar variability in N_2O emission and N stabilizers efficiency has been observed in inoculation experiments, which may be due to change of soil types (C, D) Metagenomics of in-situ soil showed that NI audition significantly changed the microbial community and functional diversity. There were differences in the response of functional genes related to nitrogen cycling to NI addition in different ecological regions, among which only the abundance of hydroxylamine oxidase gene (*hao*) was significantly increased with nitrogen fertilizer, but significantly decreased with NI addition (E) The RF and correlation analysis further verified that the hao and *Nitrosospira* carrying the *hao* gene showed a significant positive correlation with the efficiency of NI, which indicated that the *hao* gene and bacteria carrying the related genes played a significant role in the efficiency of NI on N_2O mitigation (F) In conclusion, NI is an effective tool to inhibit N_2O emission on a large regional scale, and the changes of key environmental factors and microorganisms are the main predictors of NI efficiency variation.

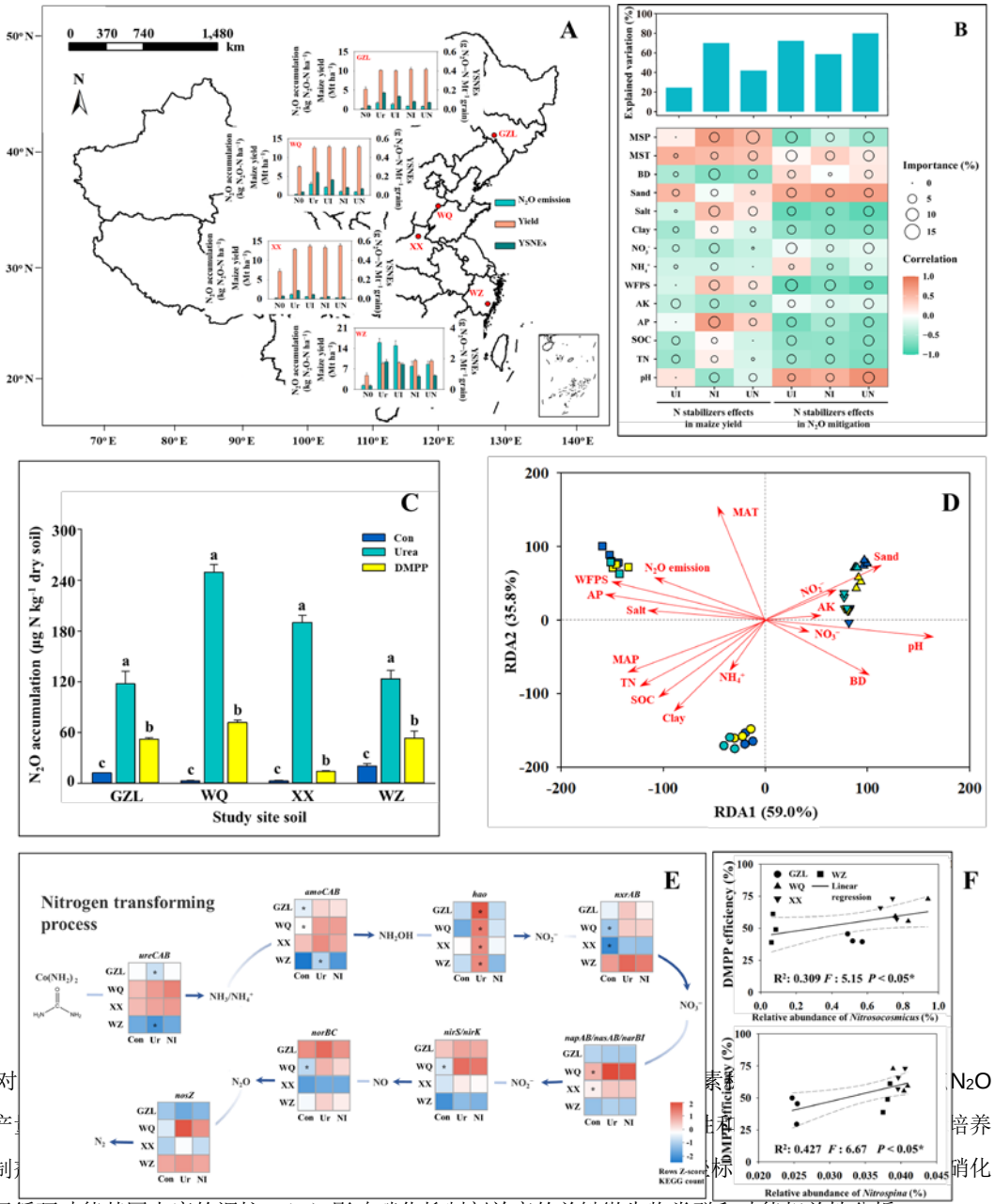


图3、氮稳定剂对[illegible]素[illegible]、N_2O排放、产量和产[illegible]性[illegible]培养条件下硝化抑制[illegible]标[illegible]硝化抑制剂对土壤氮循环功能基因丰度的调控；（F）影响硝化抑制剂效率的关键微生物类群和功能相关性分析。

Figure 3. The regulation of nitrogen stabilizers on maize field of N_2O emissions across three ecological regions and its microbial response. (A) The effects of N stabilizers on N_2O emission, maize yield, and yield-scale N_2O emission. (B) Associations of soil physicochemical properties and climatic variables with the effects of N stabilizers on maize yield and N_2O mitigation based on correlation and random forest regression model. (C) Incubation experiment of nitrification inhibitor affect N_2O emission. (D) Principal coordinates analysis (PCoA) of microbial compositions and functional compositions. (E) The relative abundance of key functional genes of nitrogen transforming process. (F) Ecological relationships between relative abundance of key taxonomic taxa, functional genes and DMPP efficiency.

（二） 研究成果

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

1. Yu K, Liu Y, Gong Z, Liang Y, Du L, Zhang Z, Li K, Pang S, Li X, Zhang L, Tan W, **Du M***, Tian X, **Li Z** (2022) Chemical topping improves the efficiency of spraying harvest aids using unmanned aerial vehicles in high-density cotton. ***Field Crop Res*** 283: 108546.
2. Yu K, Li K, Wang J, Gong Z, Liang Y, Yang M, Sun H, Zheng J, Li X, Wang L, Zhang L, Du M*, Tian X, **Li Z** (2022) Optimizing the proportion of thidiazuron and ethephon compounds to improve the efficacy of cotton harvest aids. ***Ind Crop Prod*** 191: 115949.
3. Li F, Wu Q, Liao B, Yu K, Huo Y, Meng L, Wang S, Wang B, Du M, Tian X, Li Z (2022) Thidiazuron promotes leaf abscission by regulating the crosstalk complexities between ethylene, auxin, and cytokinin in cotton. ***Int J Mol Sci*** 23: 2696.
4. Liu C, Zhang Y, Liu H, Liu X, Ren D, Wang L, Guan D, **Li Z**, **Zhang M** (2022) Fertilizer stabilizers reduce nitrous oxide emissions from agricultural soil by targeting microbial nitrogen transformations. ***Sci Total Environ*** 806: 151225.
5. Liu C, Ren D, Liu H, Liu X, Zhang Y, Wang L, **Li Z**, **Zhang M** (2022) Optimizing nitrogen management diminished reactive nitrogen loss and acquired optimal net ecosystem economic benefit in a wheat-maize rotation system. ***J Clean Prod*** 331: 129964.

专利申请：

1. 棉花丝/苏氨酸蛋白磷酸酶 GhTOPP6 及其编码基因和应用。申请人：**李召虎**，李芳军，周琳，**田晓莉**；专利号：ZL202010985865.3；授权日期：2022 年 08 月 16 日；中国，发明专利。
2. Method for Improving Sensitivity of Plant to Gibberellin Inhibitor and use thereof. 申请人：**李召虎**，张娟，李芳军，**张明才**，杜明伟，**田晓莉，段留生**；专利号：US11242537B2；授权日期：2022 年 02 月 08 日；美国，发明专利。
3. 棉花丝/苏氨酸蛋白磷酸酶 GhTOPP4 及其编码基因和应用。申请人：**李召虎，**李芳军，周琳，王玉贤，**田晓莉**；专利申请号：202211099398.X；专利申请日：2022 年 09 月 08 日；中国，发明专利。

获得奖励：

中国棉花系统调控轻简栽培技术体系的创建与应用．2021-T-03-D01．李召虎， 董合忠，田晓莉，李亚兵，李存东，张旺锋，李雪源，王林，杜明伟，代建龙。第 12 届大北农科技奖特等奖. 2022。（三） 研究队伍

固定人员：

李召虎（课题组长），张明才，田晓莉，杜明伟，李芳军，张钰石。

研究生：

刘雪晴，刘洪润，姚青青，万家驰，肖爽，隋一平，王玉贤，曹鹏飞，高先原，张特，赵淼，余明

龙，朱明媛，王瑶，黄明远，王万新，谢润之。

孙传清课题组

孙传清，教授。

研究方向：（1）水稻株型、产量、耐逆性状驯化与遗传调控机理；（2）野生稻优异基因克隆与利用。

（一） 研究进展

多胺氧化酶 OsPAO3 调控水稻萌发期耐盐性

土壤盐渍化是农业生产持续发展的主要制约因素之一。盐胁迫抑制作物生长发育，导致存活率、

生物量和产量的显著降低。水稻在萌发期对盐胁迫较为敏感，高盐胁迫将抑制种子萌发，降低幼苗存活率，严重影响水稻生产。因此，鉴定水稻萌发期耐盐基因，解析萌发期盐胁迫响应分子机理，为培育耐盐水稻品种提供基因资源具有重要意义。

该研究以籼稻品种特青为遗传背景的云南元江普通野生稻渗入系为研究材料，通过萌发期耐盐性鉴定，筛选出 1 个盐敏感渗入系 YIL3。利用该渗入系与受体亲本特青回交构建的分离群体，采用图位克隆技术克隆了水稻萌发期耐盐基因 *OsPAO3*，该基因编码多胺氧化酶，在水稻多个组织中表达且盐胁迫处理时上调表达。过量表达 *OsPAO3* 基因可提高种子胚芽鞘中多胺的含量，进而增强 ROS 清除酶活性，消除过度积累的 H_2O_2，降低种子胚芽鞘中的 Na^+含量，通过维持离子平衡，削弱 Na^+积累导致的细胞损伤，最后提高了水稻种子萌发期的耐盐性（图 1）。研究结果不仅为水稻耐盐品种的培育提供了新的基因资源，亦为水稻耐盐机理研究提供了线索（Liu et al., *J Genet Genomics*, 2022）。

Polyamine Oxidase 3 is Involved in Salt Tolerance at the Germination Stage in Rice

Soluble salts are present in widespread saline soils and accumulate in the subsoil of agricultural areas owing to poor water management. They cause salt stress that inhibits growth and reduces yield of crops. Rice, one of the most important food crops, is salt-sensitive in the early seedling stages, but commonly suffers salt stress because of irrigation-dependent tillage patterns. Identification of genes associated with salt tolerance at the germination stage in rice will benefit efforts for enhancing tolerance to saline farmland and expanding utilization of saline soil.

Here, we identified a polyamine oxidase gene, *OsPAO3*, conferring salt tolerance at the germination stage in rice (*Oryza sativa* L.), through map-based cloning approach. *OsPAO3* is up-regulated under salt stress at the germination stage and highly expressed in various organs. Overexpression of *OsPAO3* increased activity of polyamine oxidases, enhancing the polyamine content in seed coleoptiles. Increased polyamine may lead to the enhance of the activity of ROS-scavenging enzymes to eliminate over-accumulated H_2O_2 and the reduction of Na^+ content in seed coleoptiles to maintain ion homeostasis and weaken Na^+ damage. These changes resulted in stronger salt tolerance at the germination stage in rice. Our findings not only provide a novel gene for breeding new salt-tolerant rice cultivars but also help to elucidate the mechanism of salt tolerance in rice (Liu et al., *J Genet Genomics*, 2022).

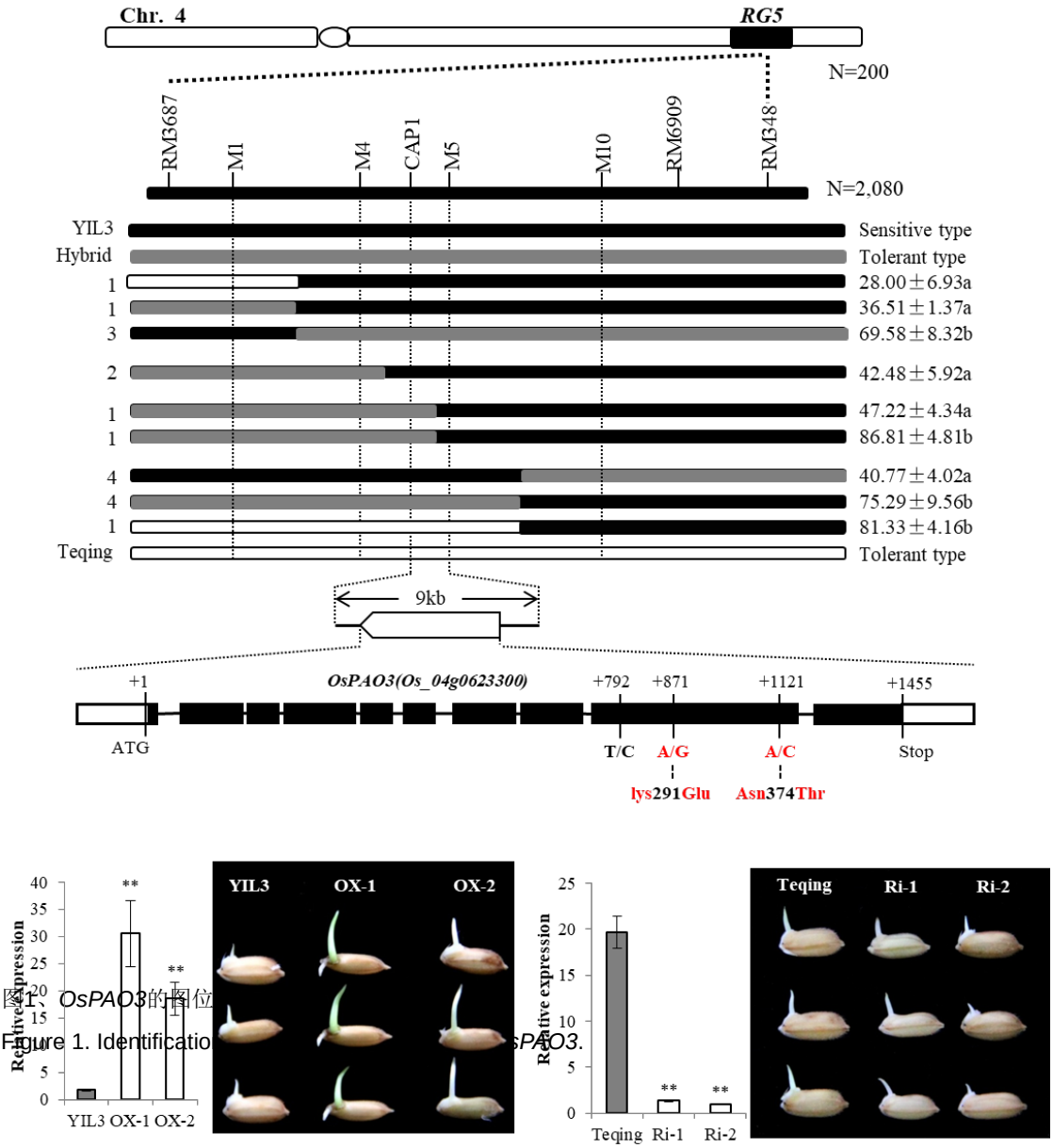


图1. *OsPAO3*的图位

Figure 1. Identificatio *sPAO3*.

（二） 研究成果

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

Liu G*, Jiang W*, Tian L, Fu Y, Tan L, Zhu Z, **Sun C***, **Liu F*** (2022) Polyamine oxidase 3 is involved in salt tolerance at the germination stage in rice. ***J Genet Genomics*** 49: 458-468.

（三） 研究队伍

固定人员：

孙传清（课题组长），刘凤霞。

研究生：

梁玮玮，邢宏伟，王欢，黄琨，满辰，苏佳乐，袁睿智，刘相麟，李晓玥，许旻毓，于利伟，王艳茹，魏茜，何萍，李瑞超，姜晚霞，段俊骅，邹俊，马聿荣，邓浩东，郭雨璐，王昕民。

段留生

课题组

段留生，教授。

研究方向：作物抗逆高效性状的化调控技术及应用。

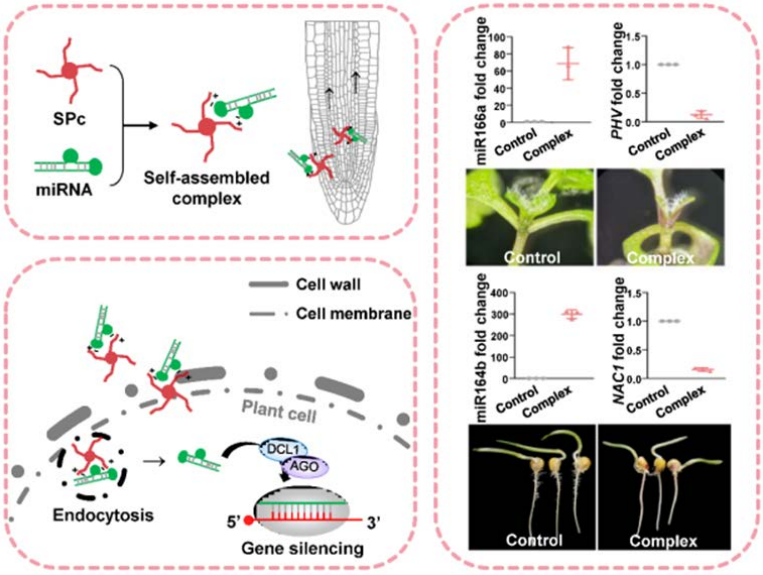
（一） 研究进展

1、玉米 Nano-miRNA 体外递送系统的创建

MicroRNA 通过靶向mRNA切割抑制靶基因的翻译，在植物生长发育和抗逆过程中发挥着重要作用。近年来体外递送miRNA精准调控基因表达在农业生产上进展缓慢，因此如何提高miRNA的体外递送效率是目前该领域的难题之一。本研究借助纳米技术探究纳米载体SPc与MIRNA的结合能力及其递送ds-MIRNA进入植物细胞的效率，结果表明：1. 纳米载体SPc与ds-MIRNA能够结合形成稳定的复合物，最佳质量比为1:1，复合物形态为小于20 nm的球形纳米颗粒。2. 纳米载体SPc可以有效地递送ds-MIRNA进入拟南芥根系和微创玉米根系中。通过荧光标记追踪ds-MIRNA/SPc内化情况，信号均显著高于清水处理和单独荧光标记的ds-MIRNA。3. 纳米载体SPc递送ds-MIRNA进入植物体内，能够高效切割靶基因，调控拟南芥和玉米的形态建成，表现出与MIRNA过表达材料相似的表型。本研究首次尝试在主要作物玉米上借助纳米载体构建miRNA的体外递送技术，为开发小RNA类植物生长调节剂奠定基础（Yang et al., *J Nanobiotechnol*, 2022）。

Construction and Application of Star Polycation Nanocarrier-Based Microrna Delivery System in *Arabidopsis* and Maize

Micro RNA (miRNA) plays vital roles in the regulation of both plant architecture and stress resistance through cleavage or translation inhibition of the target messenger RNAs (mRNAs). In recent years, how to improve the efficiency of miRNA delivery in vitro is one of the current challenges in this field. In this study, the binding ability of SPc to ds-MIRNA and its delivery efficiency of delivering ds-MIRNA into plant cells were investigated. The following results were obtained: 1.SPc could assemble with ds-MIRNA through electrostatic interaction to form nano-sized ds-MIRNA/SPc complex. The best mass ratio was 1:1 through the electrostatic



interaction. The complexes morphology is spherical nanoparticles with small particle size below 20 nm. 2.The formed nano-sized ds-MIRNA/SPc complex could penetrate the root cortex and be systematically transported through the vascular tissue in seedlings of *Arabidopsis* and maize. Internalization of ds-MIRNA/SPc was traced by fluorescent labeling, and the fluorescent signal was significantly higher in both *Arabidopsis* and minimally invasive maize root systems. 3. SPc-delivered ds-MIRNA could efficiently increase mature miRNA amount to suppress the target gene expression in *Arabidopsis* and maize, and the similar phenotypes of *Arabidopsis* and maize were observed compared to the transgenic plants overexpressing miRNA. To our knowledge, we report the first construction and application of star polycation nanocarrier-based platform for miRNA delivery in plants, which explores a new enable approach of plant biotechnology with efficient transformation for agricultural application (Yang et al., *J Nanobiotechnol*, 2022).

图1、基于SPc纳米载体的miRNA递送系统在拟南芥和玉米中的应用。

Figure 1. Application of nanocarrier-based microRNA delivery system in *Arabidopsis* and maize.

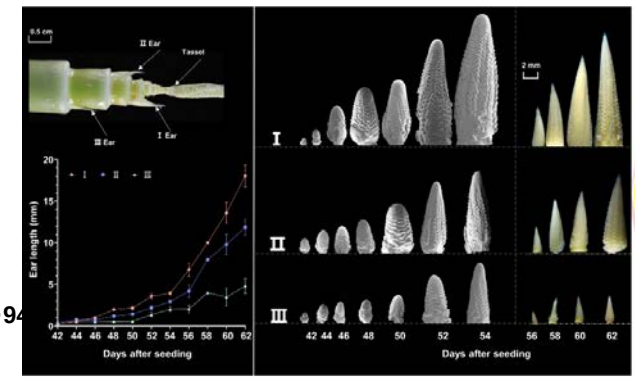
2、玉米早期不同部位雌穗发育的转录组动态分析

穗发育情况是影响玉米产量的重要因素。在玉米生长早期，所有的腋生分生组织都有发展成类似花序分生组织（IM）并从 IM 进行繁殖的潜力。但在大多数情况下，只有一个或两个雌穗可以产

生花丝正常授粉结实。为了探索不同穗之间发育过程中的变化和相互作用，研究在 11 个时间点对玉米前三穗进行了高时间分辨率转录组学研究并结合生长进程将玉米早期穗发育划分为 3 个阶段。在玉米穗发育早期一共检测到 23,821 个表达基因，包括 1,876 个转录因子（TFs）。其中，5,855 个基因在第一、二、三穗的生长过程中显著差异表达，差异表达较多的基因集中在花器官发育起始阶段（播种后 56-62 天）。本文报道的高时间分辨率转录组图谱为揭示早期不同部位雌穗花序发育的遗传调控机制提供了重要的功能资源。总的来说，在 IM 发育到小穗对分生组织（SPM）阶段，1、2、3 穗形态与基因表达的相似性说明，每个穗原基都有具备发育成穗的基础条件；正常的穗发育过程需要充足养分供应以及 IAA、GA 等激素的正向调节；3 穗的衰退是一个逐步加重的过程，由营养缺失、ETH 和 JA 等过量积累导致。

Dynamic Transcriptome Landscape of Early Different Axillary Female Inflorescences Development in Maize

Ear development is an important factor related to maize (Zea mays L.) yield. At the early stage of maize growth, all axillary meristems had the potential to develop into similar inflorescence meristem (IM) and then to reproduce from IM. But in most cases, only one or two top ears can generate silks at anthesis. To explore the changes and interactions between different panicles during development, we sampled the top three ears of maize at eleven time points for high time resolution transcriptomics studies. A total of 23,821 expressed genes including 1,876 transcription factors (TFs) were detected in early stages of maize ear development. Of these genes, 5,855 were significantly differentially expressed in the growth of the first, second and third ears, with more differentially expressed genes concentrated in the stage of initiation of flower organ development (56 DAS to 62 DAS). The high temporal-resolution transcriptome atlas reported here provides an important functional resource for uncovering the genetic regulatory mechanisms of early different axillary female inflorescences development. In general, the similarity of the morphology and gene expression of the first, second and third ears during the stage of IM development to spikelet pair meristems (SPM) indicated that each ear primordium had the basic conditions to develop into ear. Normal ear development requires adequate nutrient supply and positive regulation of auxin, gibberellin and other hormones. The decline of the third ear is a gradual aggravating process, which is caused by nutrient deficiency, excessive accumulation of ethylene and jasmonic acid.



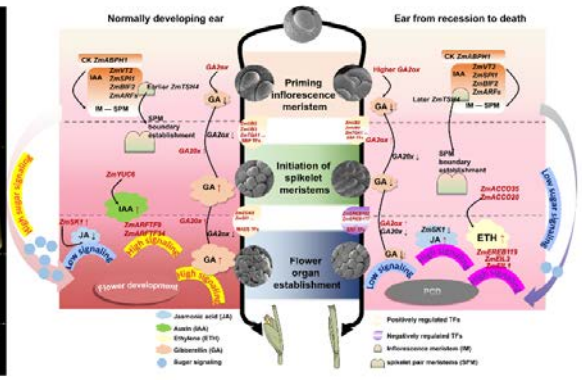


图 2、播种后 42 ~ 62 天 1、2、3 穗的变化及不同部位穗发育的调控机制。

Figure 2. Changes in first (Ⅰ), the second (Ⅱ) and third (Ⅲ) top ears from 42 to 62 days after seeding (DAS) and mechanisms regulating ear development at different positions.

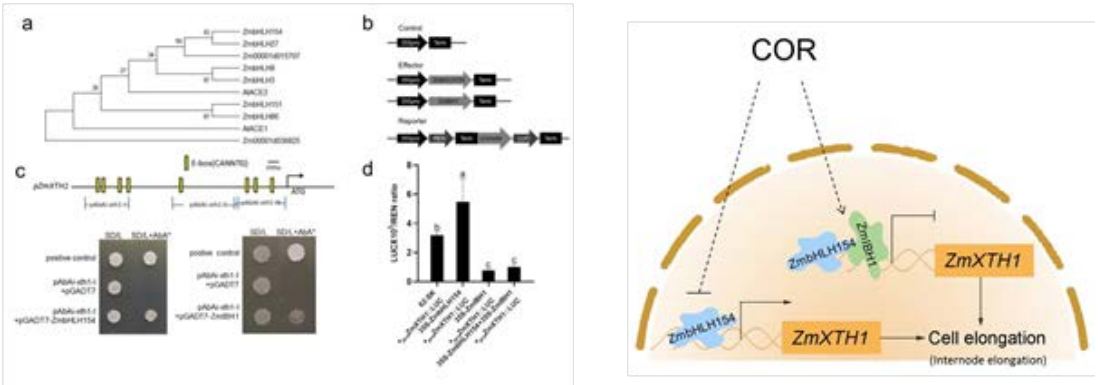
3、冠菌素调控细胞壁合成基因 *ZmXHT1* 介导玉米节间伸长的机理研究

倒伏严重制约玉米产量和机械化收货，拔节期喷施冠菌素可以有效缩短玉米基部节间长度，减少倒伏的发生。研究通过对十个不同基因型玉米进行 30 μmol·L^{-1} 冠菌素处理发现：*ZmXTH1* 在节间伸长区的表达均被显著抑制。*ZmXTH1* 编码木葡聚糖内糖基转移/水解酶（XET/XEH），在细胞壁松弛与扩张过程中发挥重要作用。*ZmXTH1* 过表达株系的株高、穗位高、以及基部节间长度相对于野生型植株显著增加。*ZmXTH1* 过表达株系茎秆内细胞长度显著增加。生化实验结果表明 ZmbHLH154 可以结合在 *ZmXTH1* 启动子的顺式结合元件 E-box 上，激活其表达，而转录抑制因子 ZmIBH1 也可以结合其启动子，表现为抑制其转录活性。此外 ZmbHLH154 与 ZmIBH1 之间也存在物理互作关系，这使得 ZmbHlH154 的转录激活活性受到显著干扰。目前正在构建 ZmbHLH154 与 ZmIBH1 的转基因材料，探究冠菌素介导的茉莉酸信号通路与这两个转录因子之间的直接关系，以期明确冠菌素调控玉米节间伸长的分子机制。

Coronatine Regulates Maize Internode Elongation by Mediates Cell Wall Development

Lodging seriously restricts maize production and mechanized harvesting. Spraying Coronatine (COR) can effectively shorten the length of basal internodes of maize and reduce the occurrence of lodging. 30 μmol·L^{-1} COR treatment significantly decreased the expression of *ZmXTH1* in the elongation region of internodes at 10 different genotypes. *ZmXTH1* encodes xyloglucan endotransglucosylase/hydrolases (XET/XEH), which acts on primary cell wall and plays an important role in cell wall relaxation and expansion. The plant height, ear height and basal Internode length of *ZmXTH1* overexpression lines were obviously higher than those of wild type plants. By anatomical analysis the 8th Internode of maize during the V13 stage, it was found that the cell length in the stem of the overexpressed lines increased significantly. The results of biochemical experiments showed that ZmbHLH154 could bind to the cis-binding element E-box of the *ZmXTH1* promoter and activate its expression, while the transcriptional inhibitor ZmIBH1 could also bind to the promoter and negatively regulate expression. In addition, ZmbHLH154 physically interacted with ZmIBH1, which significantly interferes with the transcriptional activation activity of ZmbHlH154. The current work is to construct transgenic maize of ZmbHLH154 and ZmIBH1 and explore the direct relationship between COR and these two transcription factors to clarify the molecular mechanism of COR regulating maize Internode elongation.

图 3、



Firgure 3. A working model for COR the regulation of internode elongation by influencing *ZmXTH1* expression.

（二） 研究成果

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

1. Yang J#, Yan S#, Xie S, Yin M, Shen J, Li Z, **Zhou Y** *, **Duan L*** (2022) Construction and application of star polycation nanocarrier-based microRNA delivery system in *Arabidopsis* and maize. ***J Nanobiotechnol*** 20 (1) : 219.
2. Du L, Yang Z, Zhang H, Yu K, Wang X, Tan W, **Duan L*** (2022) Design, synthesis and herbicidal evaluation of novel urea derivatives with inhibition activity to root growth. ***J Plant Growth Regul*** s00344-022-10867-z.
3. Wang W, Ren, ZB, Li L, Du YP, Zhou YY, Zhang MC, Li ZH, **Yi F***, **Duan L** (2022) Meta-QTL analysis explores the key genes, especially hormone related genes, involved in the regulation of grain water content and grain dehydration rate in maize. ***BMC Plant Biology*** 22 (1) : 346.
4. Feng TY, Zhang Y, He M , Zhang MC, Li ZH, **Zhou YY***, **Duan L*** (2022) Coronatine alleviates cold stress by improving growth and modulating antioxidative defense system in rice (*Oryza sativa* L.) seedlings. ***Plant Growth Regul*** 96 (2) : 283-291.
5. Li RQ#, Wei, ZF, Li Y, Shang XD, Cao Y, **Duan LS**, Ma LG* (2022) SKI-INTERACTING PROTEIN interacts with SHOOT MERISTEMLESS to regulate shoot apical meristem formation. ***Plant Physio*** 189 (4)：2193-2209.

专利申请与授权：

1. 一种调节植物生长的组合物及其制备方法与应用。申请人：**段留生**，于春欣，姜峰，谭伟明，

张明才，**李召虎**，周于毅，**田晓莉**；专利号：ZL202110757356.X；授权日期：2022 年 08 月 09 日。

2. 一种调节棉花株型提高抗逆性的组合物及其制备方法与应用。申请人：**段留生**，于春欣，杜明伟，谭伟明，姜峰，**田晓莉**，**李召虎**，**张明才**；专利号：ZL202110757950.9；授权日期：2022 年 08 月 09 日。

（三） 研究队伍

工作人员：

段留生（课题组长），谭伟明，周于毅，姜峰，易飞。

研究生：

硕士生：张腾，肖金钟，王卫，谢实朋，林子晴，李潞。

博士生：任照彬，彭传喜，何蕊，耿石英，郭豫灵，王兴，冯天雨，杜琳，杨佳，李天硕。

李　岩　课题组

李岩，教授。

研究方向：细胞骨架与植物顶端生长。

（一） 研究进展

AtVAMP726 与 AtSYP131 相互作用，介导花粉管顶端囊泡分泌

花粉管顶端的分泌囊泡与质膜融合是花粉管生长的关键步骤。然而，目前对花粉管顶端生长过程中SNARE复合体的组成和作用还知之甚少。在本研究中，我们通过CRISPR-Cas9构建了一个双突变体*vamp725 vamp726*。采用荧光标记结合显微镜观察、荧光素酶互补成像、免疫共沉淀和GST-pull down等方法进行研究。我们发现，R-SNAREs *AtVAMP726*和*AtVAMP725*的双突变显著抑制拟南芥花粉管的生长，减缓了花粉管顶端囊泡在质膜上的分泌。GFP-AtVAMP726主要定位于花粉管顶端的分泌囊泡和质膜。此外，AtVAMP726被发现与Qa-SNARE AtSYP131相互作用。光漂白（FRAP）荧光恢复实验表明，mCherry-AtVAMP726优先在花粉管顶端质膜中心区域与AtSYP131共定位。基于以上结果，我们认为AtVAMP726和AtSYP131可以形成相关SNARE复合体的一部分，介导花粉管顶端的囊泡分泌，而相关囊泡分泌可能主要发生在花粉管顶端质膜的中央区域。

AtVAMP726 Interacts with AtSYP131 to Mediate the Vesicle Secretion in the Pollen Tube Tip

Secretory vesicle fusion with the plasma membrane of the pollen tube tip is a key step in pollen tube growth. However, little is known about the composition and function of the SNARE complex during pollen tube tip growth. In this study, we constructed a *Arabidopsis* double mutant *vamp725 vamp726* via CRISPR-Cas9. Fluorescence labeling combined with microscopic observation, luciferase complementation imaging, co-immunoprecipitation and GST pull-down were applied in the study. We show that double mutation of the R-SNAREs AtVAMP726 and AtVAMP725 significantly inhibits pollen tube growth in *Arabidopsis* and slows vesicle exocytosis at the apex of the pollen tube. GFP-AtVAMP726 localized mainly to secretory vesicles and the plasma membrane at the apex of the pollen tube. Furthermore, AtVAMP726 was found to interact with the Qa-SNARE AtSYP131. In addition, fluorescence recovery after photobleaching (FRAP) experiments showed that mCherry-AtVAMP726 was first colocalize with the AtSYP131 at the

central region of the pollen tube apical plasma membrane. Based on these results, we suggest that AtVAMP726 and AtSYP131 can form a part of a SNARE complex to mediate vesicle secretion at the pollen tube apex, and the vesicle secretion may mainly occur at the central region of the pollen tube apical plasma membrane.

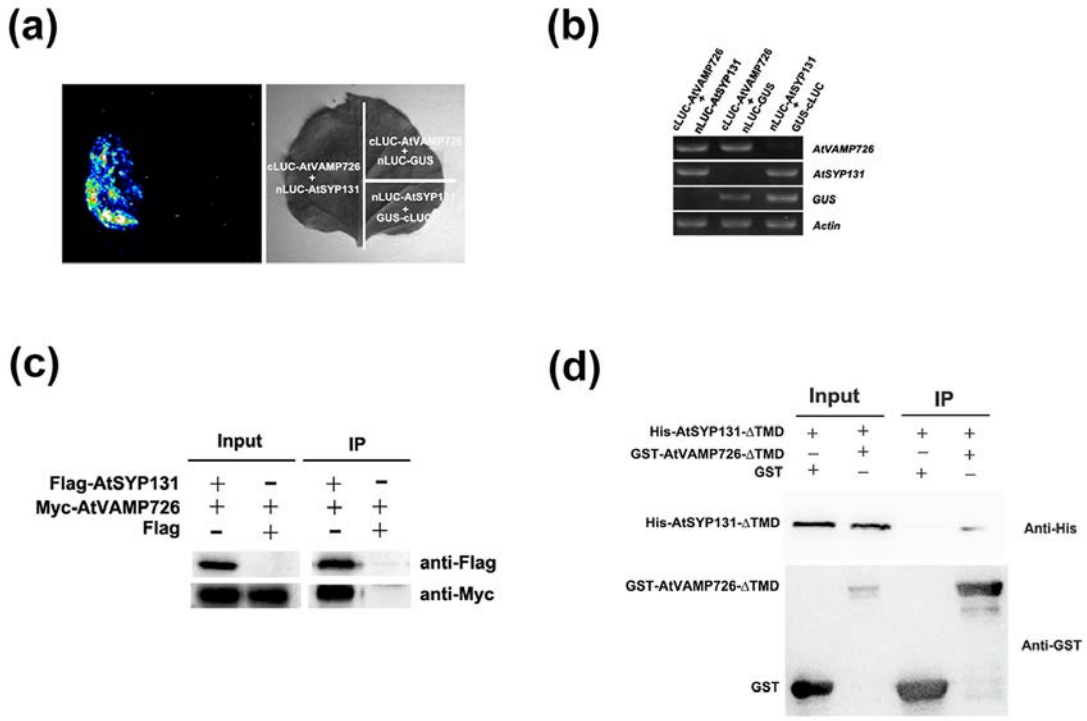


图 1、AtVAMP726 可以与 AtSYP131 互作。

Figure 1. AtVAMP726 can interact with AtSYP131.

（二） 研究成果

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

Cao Q#, Zhang W#, Liu X, **Li Y*** (2022) AtFTCD-L, a *trans*-Golgi network localized protein, modulates root growth of *Arabidopsis* in high-concentration agar culture medium. ***Planta*** 256 : 3.

（三） 研究队伍

固定人员：

李岩（课题组长）。

研究生：田绣琳，赵付丽，高亚丹。

李继刚课题组

李继刚，教授。

研究方向：光调控植物逆境响应的分子机制，植物避荫反应的分子调控机制。

（一） 研究进展

1、HY5 与 TZP 协同调控植物远红光信号传递的分子机制

在植物的遮荫环境中富含远红光，因此研究远红光信号转导的分子机制，对理解植物避荫反应的分子调控机理具有重要意义。光敏色素（phytochrome）是一类植物感知红光和远红光信号的光受体家族，而光敏色素A（phyA）是植物中唯一感受并响应远红光信号的光受体。在前期工作中，我们通过正向遗传学的方法筛选鉴定到参与植物远红光信号传递的新组分TANDEM ZINC-FINGER/PLUS3（TZP）。研究结果表明，TZP能够与远红光受体phyA相互作用，并在体内调控磷酸化phyA的产生；而磷酸化的phyA可能是活性更强的形式，在远红光信号传递中发挥重要功能（Zhang et al., *Plant Cell*, 2018; Zhou et al., *PNAS*, 2018）。然而，TZP如何整合到phyA信号调控网络中尚不清楚。在该研究中，我们发现植物光形态建成的核心正调控因子ELONGATED HYPOCOTYL5（HY5）能够直接结合*TZP*启动子上的一个G-box，并在远红光下激活*TZP*基因的表达；而突变这个G-box则使*TZP*不能在根中表达，并显著降低*TZP*在子叶和下胚轴中的表达水平。有趣的是，内源TZP蛋白在不同颜色的光下分别呈现不同的积累模式，表明TZP蛋白在不同光条件下存在不同的修饰。此外，TZP能够与调控植物光形态建成的著名E3泛素连接酶CONSTITUTIVE PHOTOMORPHOGENIC1（COP1）直接相互作用。COP1能够直接泛素化HY5，使其通过26S蛋白酶体途径降解；而TZP与COP1的相互作用能够竞争COP1与HY5的互作，从而在翻译后水平促进HY5在远红光下的蛋白稳定性。进一步研究发现，TZP自身也作为COP1的底物，在远红光和黑暗下被COP1降解。遗传分析结果表明，*tzp hy5*双突变体在低光强远红光下与*hy5*单突变体的表型相一致，但是在高光强远红光下发育出比*hy5*和*tzp*单突变体更长的下胚轴，表明在高光强远红光下TZP和HY5具有相对独立的调控功能。综上，该研究阐明HY5和TZP既相互促进，又独立发挥功能，协同调控植物的远红光信号转导途径（图1）。该研究揭示了HY5和TZP这两个远红光信号途径重要正调控因子的相互关系，为解析复杂而微妙的phyA信号调控网络提供了新的见解（Li et al., *Plant Cell*, 2022）。

Mutual Upregulation of HY5 and TZP in Mediating Phytochrome a Signaling

Phytochrome A (phyA) is the far-red (FR) light photoreceptor in plants that is essential for seedling de-etiolation under FR-rich environments, such as canopy shade. TANDEM ZINC-FINGER/PLUS3 (TZP) was recently identified as a key component of phyA signal transduction in *Arabidopsis thaliana*; however, how TZP is integrated into the phyA signaling networks remains largely obscure. Here, we demonstrate that ELONGATED HYPOCOTYL5 (HY5), a well-characterized transcription factor promoting photomorphogenesis, mediates FR light induction of *TZP* expression by directly binding to a G-box motif in the *TZP* promoter. Furthermore, TZP physically interacts with CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1), an E3 ubiquitin ligase targeting HY5 for 26S proteasome-mediated degradation, and this interaction inhibits COP1 interaction with HY5. Consistent with those results, TZP post-translationally promotes HY5 protein stability in FR light, and in turn, TZP protein itself is destabilized by COP1 in both dark and FR light conditions. Moreover, *tzp hy5* double mutants display an additive phenotype relative to their respective single mutants under high FR light intensities, indicating that TZP and HY5 also function in largely independent pathways. Together, our data demonstrate that HY5 and TZP mutually upregulate each other in transmitting the FR light signal, thus providing insights into the complicated but delicate control of phyA signaling networks (Li et al., *Plant Cell*, 2022).

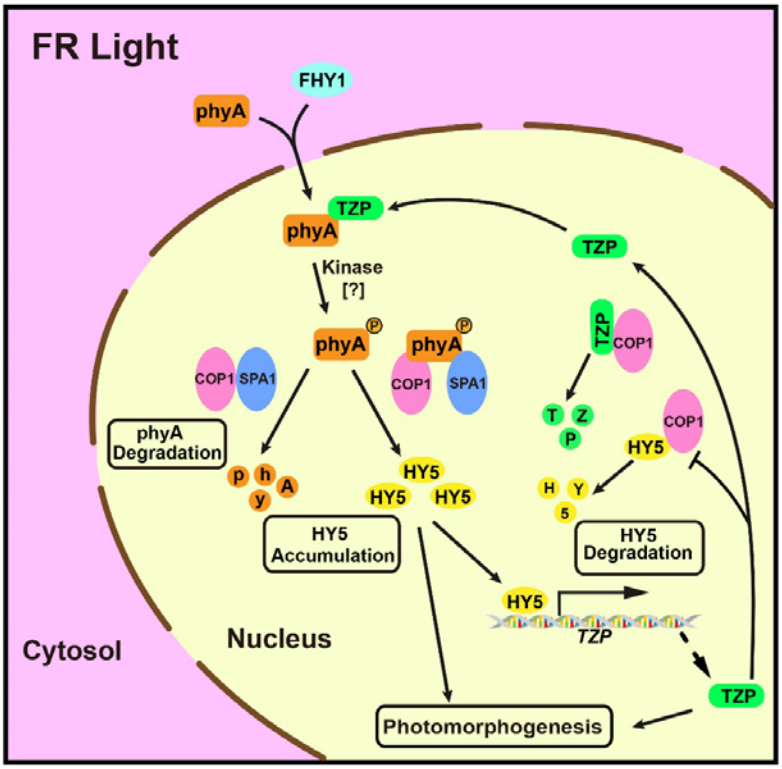


图 1、HY5 和 TZP 相互促进、协同调控植物远红光信号途径的模式图。

Figure 1. Working model depicting the mutual relationship of HY5 and TZP in phyA signaling.

2、COP1 在黑暗下介导 ABA 信号转导的分子机制

CONSTITUTIVELY PHOTOMORPHOGENIC1（COP1）是著名的E3泛素连接酶。30年来的研究表明，COP1广泛存在于真核生物中，拥有非常保守的序列特征和生化功能，在植物的整个生命周期中都发挥重要调控作用，而且哺乳动物的COP1还广泛参与到癌症发生、糖脂代谢、发育等诸多过程。在该研究中，李继刚课题组发现两个*cop1*突变体在黑暗下的幼苗生长阶段都表现出对ABA不敏感的表型。蛋白免疫印迹结果表明，ABA信号通路的重要正调控因子—ABI5在*cop1*突变体中受ABA诱导的程度显著降低，而过表达*ABI5*能够完全回补*cop1-4*突变体对ABA不敏感的表型，表明COP1可能通过促进ABA诱导ABI5蛋白积累，在黑暗下正调控植物的ABA信号途径。进一步研究发现，COP1不但促进ABA诱导*ABI5*基因的转录，还抑制ABI5经由26S蛋白酶体途径的降解，从而促进ABI5蛋白的稳定性。先前的研究表明COP1在黑暗下促进PIFs的蛋白积累，而李继刚课题组最近的研究发现PIFs直接激活*ABI5*基因的转录，此外ABI5也可以直接激活自身基因的表达，这就部分解释了为何*cop1*突变体中*ABI5*基因表达会降低。该研究接下来探索了COP1促进ABI5蛋白稳定性的分子机制。先前报道过多个能够降解ABI5的E3泛素连接酶，该研究发现COP1只和其中一个与CUL4-DDB1形成E3泛素连接酶复合体的ABD1直接相互作用。研究发现，COP1通过泛素化ABD1第122位的赖氨酸，在黑暗下促进ABD1经由26S蛋白酶体途径的降解，从而促进ABI5蛋白稳定性。有趣的是，ABA在黑暗下能够促进COP1在细胞核中积累，从而增强COP1对ABA信号的放大作用，但是ABA在光下对COP1的核质分布没有明显的调控作用。值得注意的是，*pifq*突变体（*pif1/pif3/pif4/pif5*四突变体）和*cop1*突变体在黑暗下均对ABA不敏感。该研究比较了生长在光下和暗下的野生型拟南芥对不同浓度ABA的响应，发现植物在光下确实对ABA有更强的耐受性，这可能是光受体照光激活后抑制COP1和PIFs这两类光形态建成负调控因子的结果。综上，该研究揭示了COP1通过转录和翻译后水平的双重调控机制，促进ABA对*ABI5*基因表达和蛋白水平的诱导，从而在黑暗下正调控ABA信号转导途径（图2）。该研究还揭示植物会根据环境的光信号调整其内源的ABA信号途径，从而对环境有更强的适应性，最终在自然界获得更好的生存能力（Peng et al., *Plant Cell*, 2022）。

COP1 Positively Regulates ABA Signaling During *Arabidopsis* Seedling Growth in Darkness by Mediating ABA-Induced ABI5 Accumulation

CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), a well-characterized E3 ubiquitin ligase, is a central repressor of seedling photomorphogenic development in darkness. However, whether COP1 is involved in modulating abscisic acid (ABA) signaling in darkness remains largely obscure. Here, we report that COP1 is a positive regulator of ABA signaling during *Arabidopsis* seedling growth in the dark. COP1 mediates ABA-induced accumulation of ABI5, a transcription factor playing a key role in ABA signaling, through transcriptional and post-translational regulatory mechanisms. We further show that COP1 physically interacts with ABA-hypersensitive DCAF1 (ABD1), a substrate receptor of the CUL4-DDB1 E3 ligase targeting ABI5 for degradation.

Accordingly, COP1 directly ubiquitinates ABD1 in vitro, and negatively regulates ABD1 protein abundance in vivo in the dark but not in the light. Therefore, COP1 promotes ABI5 protein stability post-translationally in darkness by destabilizing ABD1 in response to ABA. Interestingly, we reveal that ABA induces the nuclear accumulation of COP1 in darkness, thus enhancing its activity in propagating the ABA signal. Together, our study uncovers that COP1 modulates ABA signaling during seedling growth in darkness by mediating ABA-induced ABI5 accumulation, demonstrating that plants adjust their ABA signaling mechanisms according to their light environment (Peng et al., *Plant Cell*, 2022).

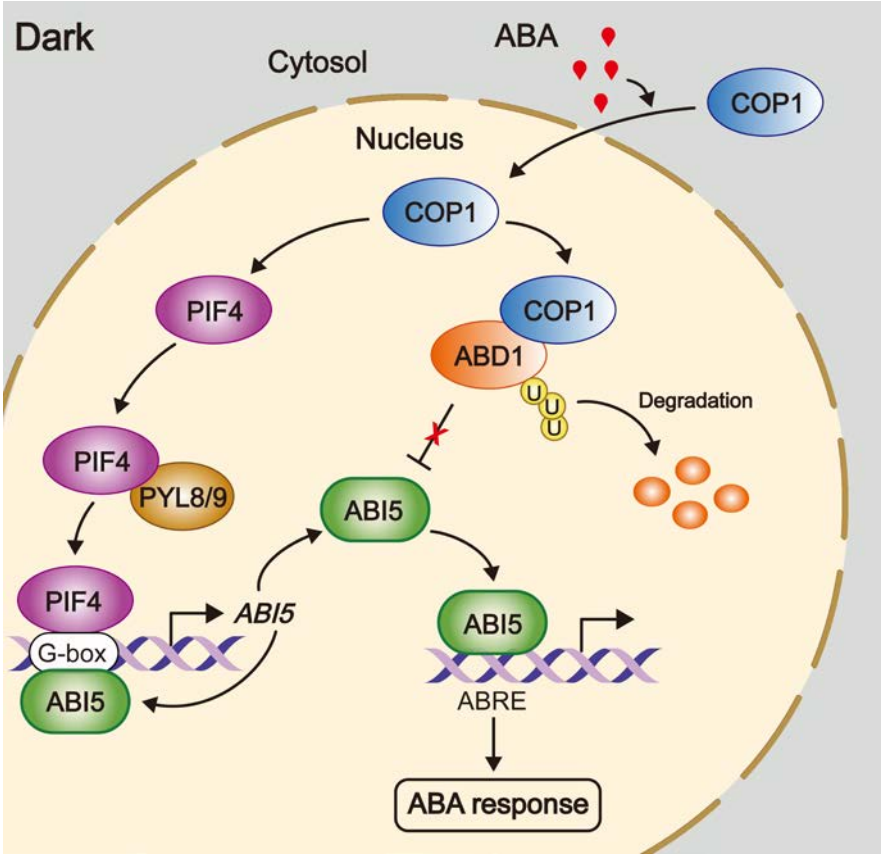


图2、COP1在黑暗下介导ABA信号转导的分子模型。

Figure 2. A working model depicting the role of COP1 in mediating ABA signaling during *Arabidopsis* seedling growth in darkness.

3、14-3-3 蛋白调控植物光形态建成的分子机制

14-3-3s 是高度保守并在真核生物中普遍存在的一类调节蛋白，能够结合磷酸化的目标蛋白，但是 14-3-3s 在植物光信号转导中的作用并不清楚。通过酵母双杂交互作验证，发现两个 14-3-3s 成员 λ 与 κ 能够与 PIF3 相互作用，并且 PIF3 bHLH 结构域上第 344 位丝氨酸对于 14-3-3λ/κ 与 PIF3 的互作起关键作用。表型分析结果显示，*14-3-3λ/κ* 双突变体在各种光下的下胚轴比野生型长，表明 14-3-3λ/κ 是光形态建成的正调控因子。此外，*14-3-3λ/κ* 的基因表达受光调控，而且有意思的是光

能够迅速诱导 14-3-3λ 蛋白的磷酸化。进一步研究表明，14-3-3λ/κ 与被 PPKs 磷酸化后的 PIF3 互作更强。蛋白免疫印迹实验结果表明，照射红光后 14-3-3λ/κ 促进 PIF3 在体内的磷酸化和降解，且该调控功能依赖于 PPKs 对 PIF3 S344 位点的磷酸化。该研究还发现 14-3-3λ/κ 能够与 phyB 互作，且与 Pfr 形式的 phyB 互作更强，并且能够促进照光之后 phyB 在细胞核中的积累。更重要的是，14-3-3λ/κ 能够促进 PIF3-PPK 及 PIF3-phyB 的互作，从而促进照光之后 phyB-PIF3-PPK 三分子复合体的形成。综上，本研究发现 14-3-3λ/κ 能够与磷酸化的 PIF3 和光激活的 phyB 互作，促进 phyB-PIF3-PPK 三分子复合体的形成，从而促进 PIF3 在照光之后快速磷酸化和降解（图 3）。该研究揭示了 14-3-3s 调控植物光形态建成的分子功能，为进一步解析复杂且精细的光信号调控网络提供了新的见解（Song et al., *New Phytol*, 2022）。

14-3-3 Proteins Regulate Photomorphogenesis by Facilitating Light-Induced Degradation of PIF3

14-3-3s are highly conserved phosphopeptide-binding proteins that play important roles in various developmental and signaling pathways in plants. However, although protein phosphorylation has been proven to be a key mechanism for regulating many pivotal components of the light signaling pathway, the role of 14-3-3 proteins in photomorphogenesis remains largely obscure. PHYTOCHROME-INTERACTING FACTOR3 (PIF3) is an extensively-studied transcription factor repressing photomorphogenesis, and it is well-established that upon red (R) light exposure, photo-activated phytochrome B (phyB) interacts with PIF3 and induces its rapid phosphorylation and degradation. PHOTOREGULATORY PROTEIN KINASES (PPKs), a family of nuclear protein kinases, interact with phyB and PIF3 in R light and mediate multisite phosphorylation of PIF3 in vivo. Here, we report that two members of the 14-3-3 protein family, 14-3-3λ and κ, bind to a serine residue in the bHLH domain of PIF3 that can be phosphorylated by PPKs, and act as key positive regulators of R light-induced photomorphogenesis. Moreover, 14-3-3λ and κ preferentially interact with photo-activated phyB and promote the phyB-PIF3-PPK complex formation, thereby facilitating phyB-induced phosphorylation and degradation of PIF3 upon R light exposure. Together, our data demonstrate that 14-3-3λ and κ work in close concert with the phyB-PIF3 module to regulate light signaling in *Arabidopsis* (Song et al., *New Phytol*, 2022).

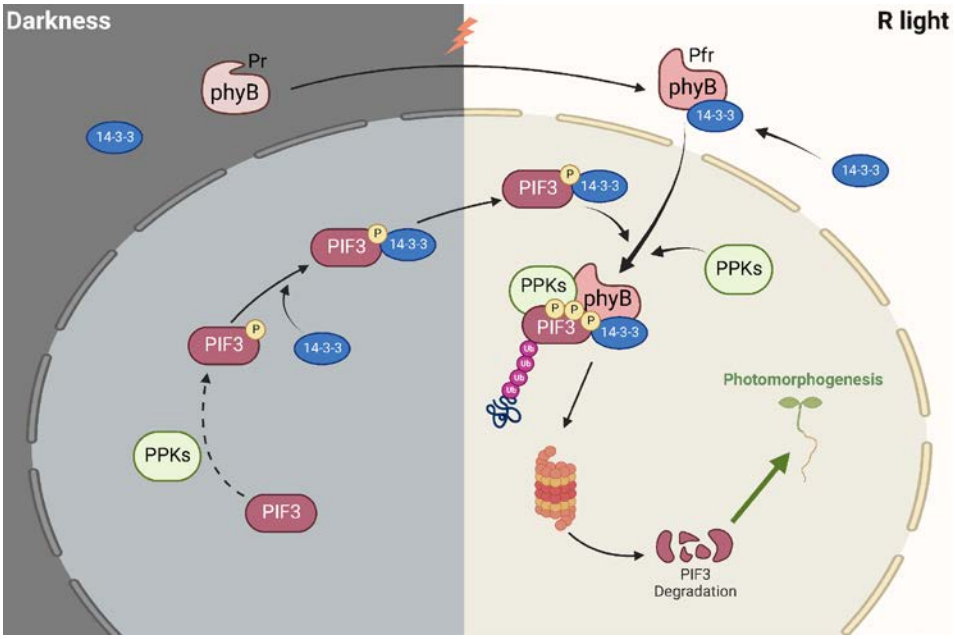


图3、14-3-3λ/κ调控植物光形态建成的工作模式图。

Figure 3. A working model depicting that 14-3-3λ and κ positively regulate R light-induced photomorphogenesis by facilitating phosphorylation and degradation of PIF3.

（二） 研究成果

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

1. Song P#, Yang Z#, Guo C, Han R, Wang H, Dong J, Kang D, Guo Y, Yang S, **Li J*** (2023) 14-3-3 proteins regulate photomorphogenesis by facilitating light-induced degradation of PIF3. ***New Phytol*** doi: 10.1111/nph.18494.
2. Peng J, Wang M, Wang X, Qi L, Guo C, Li H, Li C, Yan Y, Zhou Y, Terzaghi W, Li Z, Song CP, Qin F, Gong Z, **Li J*** (2022) COP1 positively regulates ABA signaling during *Arabidopsis* seedling growth in darkness by mediating ABA-induced ABI5 accumulation. ***Plant Cell*** 34: 2286-2308.
3. Li C#, Qi L#, Zhang S, Dong X, Jing Y, Cheng J, Feng Z, Peng J, Li H, Zhou Y, Wang X, Han R, Duan J, Terzaghi W, Lin R, **Li J*** (2022) Mutual upregulation of HY5 and TZP in mediating phytochrome A signaling. ***Plant Cell*** 34: 633-654.
4. Qi L#, Shi Y#, Terzaghi W, Yang S*****, **Li J*** (2022) Integration of light and temperature signaling pathways in plants. ***J Integr Plant Biol*** 64: 393-411.
5. Lin X*,#, Dong L#, Tang Y#, Li H#, Cheng Q, Li H, Zhang T, Ma L, Xiang H, Chen L, Nan H, Fang C, Lu S, **Li J**, Liu B*, Kong F* (2022) Novel and multifaceted regulations of photoperiodic flowering by phytochrome A in soybean. ***Proc Natl Acad Sci USA*** 119: e2208708119.
6. Wang Y, Su C, Yu Y, He Y, Wei H, Li N, Li H, Duan J, Li B, **Li J**, Davis SJ, Wang L* (2022)

TIME FOR COFFEE regulates phytochrome A-mediated hypocotyl growth through dawn-phased signaling. ***Plant Cell*** 34: 2907-2924.

7. Li T, Li H, Lian H, Song P, Wang Y, Duan J, Song Z, Cao Y, Xu D, **Li J**, Zhang H* (2022) SICKLE represses photomorphogenic development of *Arabidopsis* seedlings via HY5- and PIF4-mediated signaling. ***J Integr Plant Biol*** 64: 1706-1723.
8. 李聪，齐立娟，谷晓峰，**李继刚***（2022）植物光信号途径重要新调控因子 TZP 的研究进展. 植物学报。

（三） 研究队伍

固定人员：

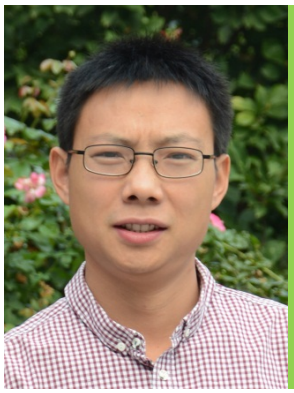
李继刚（课题组长）。

博士后：

齐立娟，韩润，彭晶。

研究生：

段杰，冯子懿，秦昕妍，吕杨，王美娇，付菁英，曹岩，陈佳琦，曹微，王淮畅，李备涵，许佳诣，刘燕，汤泽慧。



蒋才富

课题组

蒋才富，教授。

研究方向：玉米抗盐碱的应用基础研究。

（一） 研究进展

1、ZmESBL 通过调节凯氏带可塑性促进 Na^+调控和耐盐的分子机制

生长发育的可塑性调控是作物适应逆境胁迫的重要途径。凯氏带是维管植物根内皮层细胞壁径向增厚形成的特殊环状结构，其主要生理功能是阻断矿质元素通过质外体运输途径过量进出中柱。本团队的研究鉴定了一个对盐胁迫超敏感的玉米自交系 CIMBL45，发现其盐胁迫超敏感表型是由于 *ZmSTL1*（*Salt Tolerance Locus 1*）功能缺失导致。*ZmSTL1* 编码 DIR 家族蛋白 ZmESBL，CIMBL45 中一个单碱基插入导致 ZmESBL 蛋白翻译提前终止及其盐胁迫超敏感的表型，不含有该插入的 *ZmESBL* 为耐盐基因型。后续研究发现 ZmESBL 是内皮层凯氏带发育的正调控因子，通过调控凯氏带可塑性促进 Na^+调控和耐盐，其作用机制为：盐胁迫下，*ZmESBL* 表达水平增加，促进凯氏带在更靠近根尖的内皮层细胞中形成，凯氏带屏障功能增强，抑制 Na^+通过质外体途径进入中柱，从而减少 Na^+由根往地上部的转运，促进地上部 Na^+排斥和耐盐。该研究还发现拟南芥中 *ZmESBL* 的直系同源基因也参与调控凯氏带发育和盐胁迫应答，表明 ZmESBL 通过调控凯氏带的可塑性促进 Na^+调控和耐盐的机制在不同物种中可能是保守的。研究结果 2022 年 4 月发表于 *Nat Commun* 期刊。

A Dirigent Family Protein Confers Variation of Casparian Strip Thickness and Salt Tolerance in Maize

Plant salt-stress response involves complex physiological processes. Previous studies have shown that some factors promote salt tolerance only under high transpiring condition, thus mediating transpiration-dependent salt tolerance (TDST). However, the mechanism underlying crop TDST remains largely unknown. Here, we report that *ZmSTL1* (*Salt-Tolerant Locus 1*) confers natural variation of TDST in maize. *ZmSTL1* encodes a dirigent protein (termed ZmESBL) localized to the Casparian strip (CS) domain. Mutants lacking ZmESBL display impaired lignin deposition at endodermal CS domain which leads to a defective CS barrier. Under salt condition, mutation of *ZmESBL* increases the apoplastic transport of Na^+ across the endodermis, and then increases the root-to-shoot delivery of Na^+ via transpiration flow, thereby leading to a transpiration-dependent salt hypersensitivity. Moreover, we show that the ortholog of *ZmESBL*

also mediates CS development and TDST in *Arabidopsis*. Our study suggests that modification of CS barrier may provide an approach for developing salt-tolerant crops.

2、玉米 SOS 途径组分的功能变异导致耐盐性变异

经典的 SOS 信号途径参与调控细胞 Na^+外排、Na^+长距离运输等关键 Na^+稳态维持过程。迄今为止，SOS 信号途径在主要农作物中的功能及其调控 Na^+稳态的分子机制并不清楚。本团队的研究阐明了玉米中的 SOS 信号途径，揭示了 SOS 途径多个组分功能变异的分子遗传基础。该研究通过筛选玉米极端盐敏感材料，得到了一个对盐敏感的自交系 LH65，随后发现导致自交系 LH65 出现盐敏感表型的位点 *ZmSTL2*（*Salt Tolerance Locus 2*）由隐性单基因调控。*ZmSTL2* 编码 Na^+/H^+反向转运蛋白 ZmSOS1。*ZmSOS1* 最后一个外显子上的 4-bp 缺失导致 ZmSOS1 蛋白翻译提前终止。$ZmSOS1^{crispr}$ 突变体的盐敏感表型以及 *ZmSOS1* 的等位验证结果均证明自交系 LH65 的盐敏感表型是由 ZmSOS1 的功能缺失所致。在此基础上，鉴定了玉米中 SOS3 的候选组分为 ZmCBL4 和 ZmCBL8，SOS2 的候选组分为 ZmCIPK24a，并证明玉米 SOS 信号途径（ZmCBL4&ZmCBL8/ZmCIPK24a/ZmSOS1）在 Na^+稳态维持和耐盐应答中发挥重要作用。进一步研究发现部分玉米自交系中 *ZmCBL8* 的第 4 个内含子上有一个 3091-bp 的 *LTR/Gypsy* 反转录转座子插入，且该插入降低了 *ZmCBL8* 的转录水平，导致盐胁迫下玉米地上部 Na^+含量显著增加，表明该插入与 ZmCBL8 的功能变异及玉米自然群体的耐盐性变异相关。上述研究结果 2022 年 10 月发表于 *New Phytol* 期刊。

The Classical SOS Pathway Confers Natural Variation of Salt Tolerance in Maize

Sodium (Na^+) is the major cation damaging crops in the salinised farmland. Previous studies have shown that the Salt Overly Sensitive (SOS) pathway is important for salt tolerance in *Arabidopsis*. Nevertheless, the SOS pathway remains poorly investigated in most crops. This study addresses the function of the SOS pathway and its association with the natural variation of salt tolerance in maize. First, we showed that a naturally occurring 4-bp frame-shifting deletion in *ZmSOS1* caused the salt hypersensitive phenotype of the maize inbred line LH65. Accordingly, mutants lacking ZmSOS1 also displayed a salt hypersensitive phenotype, due to an impaired root-to-rhizosphere Na^+ efflux and an increased shoot Na^+ concentration. We next showed that the maize SOS3/SOS2 complex (ZmCBL4/ZmCIPK24a and ZmCBL8/ZmCIPK24a) phosphorylates ZmSOS1 therefore activating its Na^+-transporting activity, with their loss-of-function mutants displaying salt hypersensitive phenotypes. Moreover, we observed that a *LTR/Gypsy* insertion decreased the expression of *ZmCBL8*, thereby increasing shoot Na^+ concentration in natural maize population. Taken together, this study demonstrated that the maize SOS pathway confers a conservative salt-tolerant role, and the components of SOS pathway (ZmSOS1 and ZmCBL8) confer the natural variations of Na^+ regulation and salt tolerance in maize, therefore providing important gene targets for breeding salt-tolerant maize.

3、ZmHKT1;2 促进地上部 Na^+排斥的分子机制及其优异等位变异的遗传演化规律

钠离子（Na^+）是盐渍化土地中含量最丰富的可溶性阳离子，减少地上部 Na^+的积累（地上部 Na^+排斥）是作物适应高盐环境的重要途径。本团队鉴定了一个新的、促进地上部 Na^+排斥的 QTL 基因 *ZmNC3*（*Na^+ CONTENT 3*），并解析了其作用机制及其优异等位变异的遗传演化规律。该研究通过 GWAS 分析克隆了调控玉米地上部 Na^+含量的位点 *ZmNC3*。*ZmNC3* 编码细胞质膜定位的 HKT 家族离子转运蛋白 ZmHKT1;2，它具有内向 Na^+转运活性，通过将 Na^+转运至木质部薄壁细胞、加速木质部导管 Na^+卸载，从而促进地上部 Na^+排斥和玉米耐盐。后续研究发现非同义 SNP（SNP947）是导致 ZmHKT1;2 功能变异的原因，该位点为 A（编码酪氨酸）时 ZmHKT1;2 的 Na^+转运活性较低。该位点为 G（编码半胱氨酸）时 ZmHKT1;2 的 Na^+转运活性显著增强，代表了 *ZmHKT1;2* 的优异（耐盐）基因型。进一步研究表明，*ZmHKT1;2* 的优异等位变异源于大刍草，且仅有 6.1%的现代玉米种质携带该等位变异。郑单 958 的亲本郑 58 和昌 72 都不携带 *ZmHKT1;2* 的优异等位变异，通过杂交回交将 *ZmHKT1;2* 的优异等位变异导入郑 58 及昌 72 后，可显著增强其地上部 Na^+排斥能力，盐胁迫下地上部 Na^+含量减少了 50%-90%，耐盐性显著增强，表明 *ZmHKT1;2* 及其优异等位变异有良好的育种利用前景。相关研究结果 2022 年 10 月发表于 *Plant Biotechnol J* 期刊。

A Teosinte-Derived Allele of an HKT1 Family Sodium Transporter Improves Salt Tolerance in Maize

The sodium cation (Na^+) is the predominant cation with deleterious effects on crops in salt-affected agricultural areas. Salt tolerance of crop can be improved by increasing shoot Na^+ exclusion. Therefore, it is crucial to identify and use genetic variants of various crops that promote shoot Na^+ exclusion. We show that a *HKT1* family gene *ZmNC3* (*Zea mays L. Na^+ Content 3*; designated *ZmHKT1;2*) confers natural variability in shoot-Na^+ accumulation and salt tolerance in maize. *ZmHKT1;2* encodes a Na^+ -preferential transporter localized in the plasma membrane, which mediates shoot Na^+ exclusion, likely by withdrawing Na^+ from the root xylem flow. A naturally occurring nonsynonymous SNP (SNP947-G) increases the Na^+ transport activity of ZmHKT1;2, promoting shoot Na^+ exclusion and salt tolerance in maize. SNP947-G first occurred in the wild grass teosinte (at a allele frequency of 43%) and has become a minor allele in the maize population (allele frequency 6.1%), suggesting that SNP947-G is derived from teosinte and that the genomic region flanking SNP947 likely has undergone selection during domestication or post-domestication dispersal of maize. Moreover, we demonstrate that introgression of the SNP947-G *ZmHKT1;2* allele into elite maize germplasms reduces shoot Na^+ content by up to 80% and promotes salt tolerance. Taken together, *ZmNC3/ZmHKT1;2* was identified as an important QTL promoting shoot Na^+ exclusion, and its favourable allele provides an effective tool for developing salt-tolerant maize varieties.

（二） 研究成果

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

1. Zhang M#, Li Y#, Liang X, Lu M, Lai J, Song W, **Jiang C*** (2022) A teosinte-derived allele of an HKT1 family sodium transporter improves salt tolerance in maize. ***Plant Biotechnol J*** doi I: 10.1111/pbi.13927.
2. Zhou X#, Li J#, Wang Y, Liang X, Zhang M, Lu M, Guo Y, Qin F, **Jiang C*** (2022) The classical SOS pathway confers natural variation of salt tolerance in maize. ***New Phytol*** 236: 479-494.
3. Wang Y#, Cao Y#, Liang X, Zhuang J, Wang X, Qin F, **Jiang C*** (2022) A dirigent family protein confers variation of Casparian strip thickness and salt tolerance in maize. ***Nat Commun*** 13: 2222.

（三） 研究队伍

固定人员:

蒋才富（课题组长）。

博士后：

张鸣，梁晓燕，周雪雁。

科研助理：

尹攀。

研究生:

王赫扬，王立民，李芬容，王艺乔，郭辰桓，荆文琪，李雅琳，徐志鹏，叶志康，段佳宏。

张　静

课题组

张静，教授。

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

硝酸盐通过影响 NAC075 转录因子在细胞间移动而调控植物根发育

氮素是植物生长发育过程中重要的营养元素。硝酸盐不仅是陆生植物吸收氮素的主要形式，还作为重要的信号调控根系的生长发育和形态建成。根的可塑性决定植物对环境的适应性。然而，植物根系这种适应性发育的潜在分子机制仍有待研究。通过正向遗传学的方法，获得了多个主根生长对低硝酸盐胁迫敏感性降低的突变体*lonr*（*low nitrate resistant mutant*）。其中，*LONR1*编码一个转录因子NAC075。研究进一步发现，硝酸盐充足的条件下，NAC075从根中柱细胞向内皮层细胞移动。低硝酸盐胁迫可以激活CIPK1激酶活性，增加对NAC075的磷酸化，因此抑制了NAC075从中柱向内皮层的移动。滞留在中柱中的NAC075通过激活下游*WRKY53*的转录而调控低氮下根的可塑性生长。本项研究不仅完善了植物硝酸盐信号途径的调控网络，而且为基于根型改良的作物抗逆育种和氮高效育种奠定重要的理论基础。该研究成果于2022年12月在《*Developmental Cell*》上以长文形式发表（Xiao et al., *Dev Cell*, 2022）。

Nitrate Availability Controls Translocation of the Transcription Factor NAC075 for Cell-type-specific Reprogramming of Root Growth

Plant root architecture flexibly adapts to changing nitrate (NO^{3-}) availability in the soil, however the underlying molecular mechanism of this adaptive development remains understudied. To explore the regulation of NO^{3-}-mediated root growth, we screened for *low nitrate resistant mutant* (*lonr*) and identified mutants defective in the NAC transcription factor *NAC075* (*lonr1*) as being less sensitive to low NO^{3-} in terms of primary root growth. We show that NAC075 is a mobile transcription factor relocating from the root stele tissues to the endodermis based on NO^{3-} availability. Under low-NO^{3-} availability, the kinase CBL-INTERACTING PROTEIN KINASE1 (CIPK1) is activated and phosphorylates NAC075, restricting its movement from the stele, which leads to the transcriptional regulation of downstream target *WRKY53*, consequently leading to adapted root architecture. Our work thus identifies an adaptive mechanism involving translocation of transcription factor based on nutrient availability and leading to cell-specific reprogramming of plant root growth (Xiao et al., *Dev Cell*, 2022).

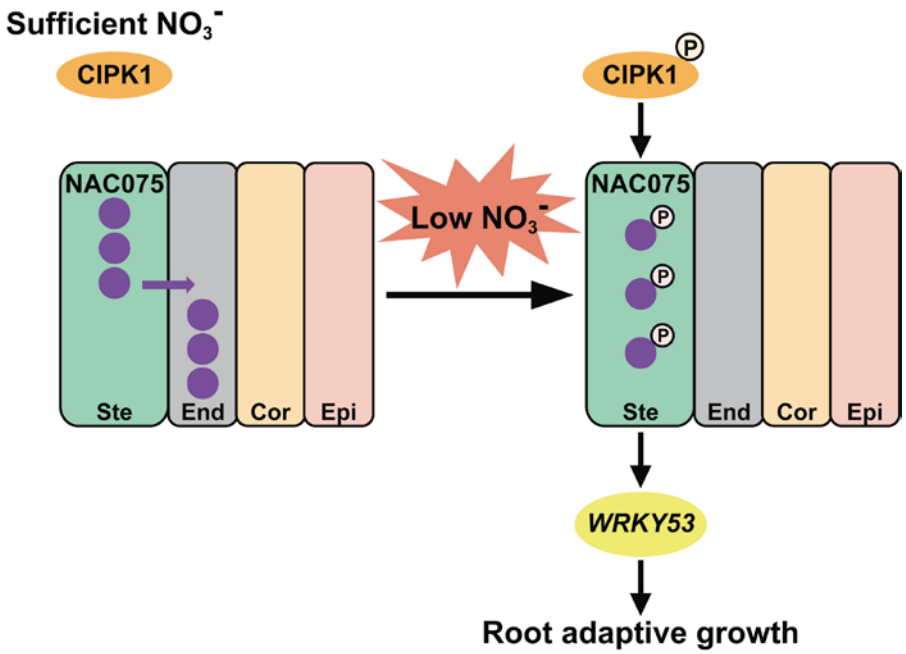


图1、转录因子NAC075调控植物响应硝酸盐根系适应性生长的分子模型。

Figure 1. A working model for NAC075-mediated root adaption in response to NO_3^- availability.

（二） 研究成果

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

Xiao H#, Hu Y#, Wang Y#, Cheng J#, Wang J, Chen G, Li Q, Wang S, Wang Y, Wang S-S, Wang Y, Xuan W, Li Z, Guo Y, Gong Z, Friml J, **Zhang J*** (2022) Nitrate availability controls translocation of the transcription factor NAC075 for cell type-specific reprogramming of root growth. ***Dev Cell*** 57: 2638-2651.

（三） 研究队伍

固定人员：

张静（课题组长）。

研究生：

贾冠南，赵雪米，袁志，陈国经纬，万璐，王锦怡，付然欣，胡玉梅，刘欣怡，刘钊，何高镜。

陈其军

课题组

陈其军，教授。

研究方向：植物生物技术。

（一） 研究进展

1、优化的引导编辑技术可以高效产生草甘膦抗性水稻

引导编辑技术是一种基于CRISPR/Cas系统的通用型精准基因组编辑技术，在植物基础研究和作物分子育种中应用潜力巨大。但由于第一代引导编辑技术在植物中的效率偏低，限制了该技术在植物中的应用。最近，哈佛大学的David Liu团队通过3种优化策略在哺乳动物细胞中大幅提高了引导编辑效率。为克服引导编辑在植物中应用的障碍，我们在水稻中测试了基于这3种策略改进的引导编辑器。EPSPS基因的TAP-IVS突变是在绿穗苋自然变异群体中发现的抗草甘膦突变，没有明显的适应性代价。为此，我们首先在水稻原生质体中对EPSPS基因TAP位点进行了引导编辑测试。结果表明，优化后的引导编辑器显著提高了TAP-IVS编辑效率。在稳定转化株系中，优化的引导编辑器（ePE3max和ePE5max）可高效产生纯合和杂合的TAP-IVS突变株系。草甘膦抗性测试表明，纯合的TAP-IVS突变体可以耐受10 mM的农用草甘膦喷施处理。这些结果为水稻非转基因草甘膦抗性育种奠定了坚实的基础。为进一步验证ePEmax系统的高效性，我们对更多的靶点进行了测试。对六种引导编辑器在20个靶点中的编辑效率进行比较分析。这些结果提示，优化的引导编辑器在水稻中的编辑效率可以达到实用化程度。与我们之前研究结果一致，我们发现除Indels外还存在两类主要的副产物：由DNA异源双链的均衡修复衍生的副产物（Re-byproducts）及源自pegRNA支架的副产物（Sc-byproducts）。我们提出了降低各类副产物的方法或建议。

Optimized Prime Editing Efficiently Generates Glyphosate-Resistant Rice Plants

Prime editing is a novel and universal CRISPR/Cas-derived precise genome-editing technology, however, low efficiency has restrained the original prime editors (PEs) from being used broadly in plants. Recently, optimized PEs have been reported to greatly improve prime editing efficiency in mammalian cells by combining three optimization strategies: engineering pegRNAs, optimizing PE protein, and manipulating cellular determinants of prime editing. In this paper, we tested the optimized PEs in rice protoplasts and transgenic lines, demonstrating that the optimized PEs greatly improved prime editing efficiency. We named the two optimized PEs ePE3max and ePE5max: the former is comprised of the PEmax protein, an engineered pegRNA with evopreQ1 appended to its 3' end, and a nicking sgRNA; the latter is comprised of the

ePE3max system and a dominant negative OsMLH1 variant for inhibiting DNA mismatch repair. Using the two optimized PEs, we efficiently generated homozygous and heterozygous TAP-IVS mutation in *EPSPS* and demonstrated that the mutation conferred glyphosate-resistance in rice. In addition, we demonstrate that using the rule of termination to re-design pegRNAs was able to eliminate the pegRNA scaffold-derived byproducts, which increased along with enhanced prime editing efficiency. Collectively, our results demonstrate that the optimized PEs are now able to remove the main obstacle to broad applications of prime editing in rice and lay a solid foundation for rice non-transgenic glyphosate-resistance breeding.

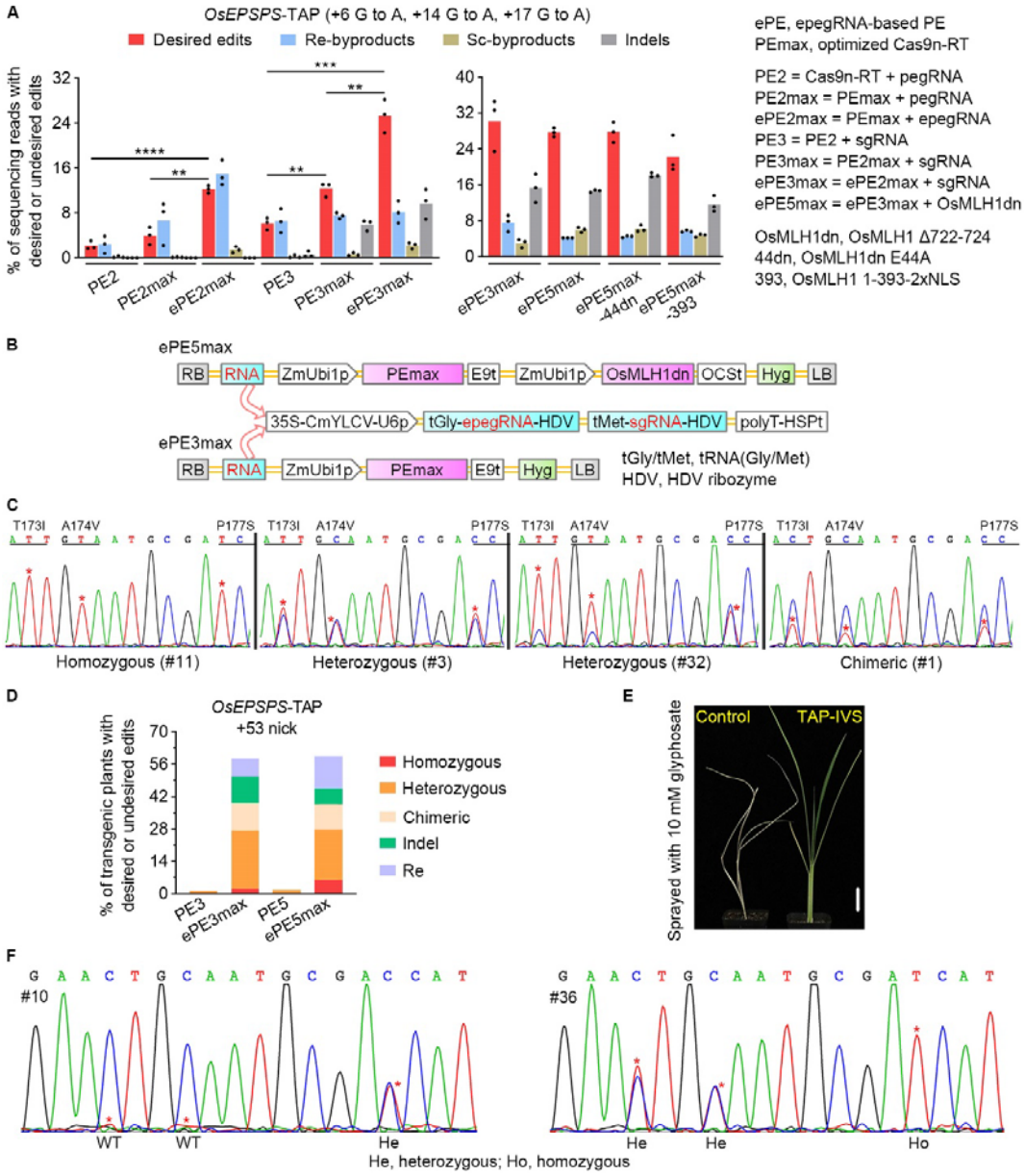


图1、优化的引导编辑技术可以高效产生草甘膦抗性水稻。

Figure 1. Optimized prime editing efficiently generates glyphosate-resistant rice plants.

2、优化的引导编辑技术在玉米中高效了产生可遗传的突变

引导编辑在玉米中应用的主要障碍是编辑效率偏低。最近，在三个方面得到优化的引导编辑器其编辑效率在动物细胞和水稻中得到大幅提高。在本研究中，我们在玉米中测试了基于这三个策略优化的引导编辑器。我们针对三类除草剂作用靶基因进行引导编辑的结果表明，ePE5max 系统可以在玉米中高效产生可遗传的突变，突变体株系表现出预期的抗除草剂表型。我们的结果证实，ePE5max 系统可以在玉米中足够高效地产生可遗传突变，解决了引导编辑在玉米中应用的主要障碍。

Optimized Prime Editing Efficiently Generates Glyphosate-Resistant Rice Plants

Low efficiency is the main obstacle to using prime editing in maize (*Zea mays*). Recently, prime-editing efficiency was greatly improved in mammalian cells and rice (*Oryza sativa*) plants by engineering prime editing guide RNAs (pegRNAs), optimizing the prime editor (PE) protein, and manipulating cellular determinants of prime editing. In this study, we tested PEs optimized via these three strategies in maize. We demonstrated that the ePE5max system, composed of PEmax, epegRNAs (pegRNA-evopreQ1), nicking single guide RNAs (sgRNAs), and MLH1dn, efficiently generated heritable mutations that conferred resistance to herbicides that inhibit 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), acetolactate synthase (ALS), or acetyl CoA carboxylase (ACCase) activity. Collectively, we demonstrate that the ePE5max system has sufficient efficiency to generate heritable (homozygous or heterozygous) mutations in maize target genes and that the main obstacle to using PEs in maize has thus been removed.

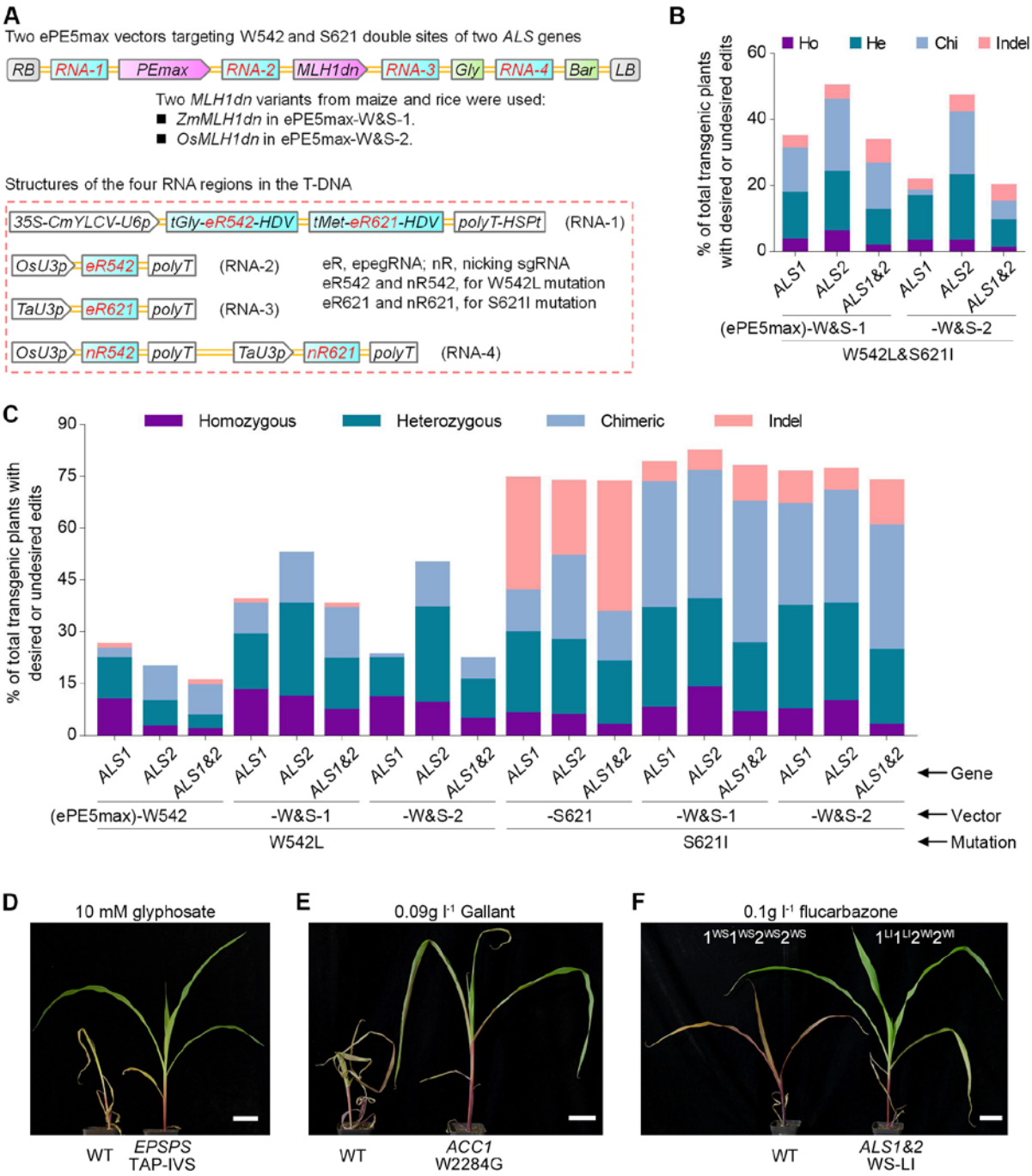


图2、靶向两个基因各两个靶点的ePE5max系统的编辑效率以及T1突变体的除草剂抗性分析。

Figure 2. Editing efficiency of the ePE5max system targeting two sites for two genes and herbicide resistance analysis of the resulting T1 mutants.

（二） 研究成果

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

1. Jiang Y#, Chai Y#, Qiao D, Wang J, Xin C, Sun W, Cao Z, Zhang Y, Zhou Y, Wang XC, **Chen QJ*** (2022) Optimized prime editing efficiently generates glyphosate-resistant rice plants carrying homozygous TAP-IVS mutation in EPSPS. ***Mol Plant*** 15: 1646-1649.

2. Qiao D[#], Wang J[#], Lu M[#], Xin C, Chai Y, Jiang Y, Sun W, Cao Z, Guo S, Wang XC, **Chen QJ***(2022) Optimized prime editing efficiently generates heritable mutations in maize. ***J Integr Plant Biol*** Accepted.

（三） 研究队伍

固定人员：

陈其军（课题组长）。

研究生：

张钰，姜媛媛，柴一萍，乔德鑫，王俊雅，辛翠平，曹正宏，孙炜，芦钰。

齐俊生课题组

齐俊生，研究员。

研究方向：作物抗逆高效的分子设计和种质创新。

（一） 研究进展

重组酶介导多基因在棉花中的聚合

利于本实验室专利基因 *VDAL*、*GbLTP3* 及 *GbAt11* 叠加培育出了抗黄萎病株系。位点特异性基因叠加可以减少分离位点的数量，加快转基因从品系向田间种植品系的进度。重组酶介导的位点特异性基因叠加提供了灵活有效的解决方案，但这种方法需要基因组中的重组酶识别位点。本文描述了几种适合于分枝杆菌 Bxb1 重组酶介导基因叠加的棉花品系（*Gossypium hirsutum cv.Coker 312*）。通过随机插入事件的筛选，获得了目标株系，每一个株系都包含有 RS2、lox 和 attP 位点靶标的单个完整拷贝，且未插入已知基因内部或着丝粒附近，结果显示报告基因 GFP 可以正常表达。本研究利用 3 个抗黄萎病候选基因（***VDAL GbLTP3* 及 *GbAt11*，本实验室专利基因，齐俊生标注**）的不同组合插入 3 个棉花目标系（CTS1、CTS3 和 CTS4）进行了基因叠加测试。从 95 个独立转化的胚性愈伤组织中获得了 9 个位点特异性整合事件。再生植物的 Southern 和 DNA 序列分析证实了精确位点的特异性整合，并发现 **CTS1i3** 植株**对黄萎病的有效抗性**得以提高，且具有位点特异性单一拷贝。这些棉花目标系可作为重组酶介导的基因叠加的基础株系，为精准 DNA 整合及遗传育种奠定了基础（Li et al., *Plant Physio.,* 2022）。

Recombinase-Mediated Gene Stacking in Cotton

Site-specific gene stacking could reduce the number of segregating loci and expedite the introgression of transgenes from experimental lines to field lines. Recombinase-mediated site-specific gene stacking provides a flexible and efficient solution, but this approach requires a recombinase recognition site in the genome. Here, we describe several cotton (*Gossypium hirsutum cv. Coker 312*) target lines suitable for Mycobacteriophage Bxb1 recombinase-mediated gene stacking. Obtained through the empirical screening of random insertion events, each of these target lines contains a single intact copy of the target construct with precise sequences of RS2, lox, and attP sites that is not inserted within or close to a known gene or near a centromere and shows good expression of the reporter gene gfp. Gene stacking was tested with insertion of different combinations of three candidate genes for resistance to verticillium wilt into three cotton

target lines: CTS1, CTS3, and CTS4. Nine site-specific integration events were recovered from 95 independently transformed embryogenic calluses. Southern and DNA sequence analyses of regenerated plants confirmed precise site-specific integration, and resistance to verticillium wilt was observed for plant CTS1i3, which has a single precise copy of site-specifically integrated DNA. These cotton target lines can serve as foundation lines for recombinase-mediated gene stacking to facilitate precise DNA integration and introgression to field cultivars (Li et al., *Plant Physio.*, 2022).

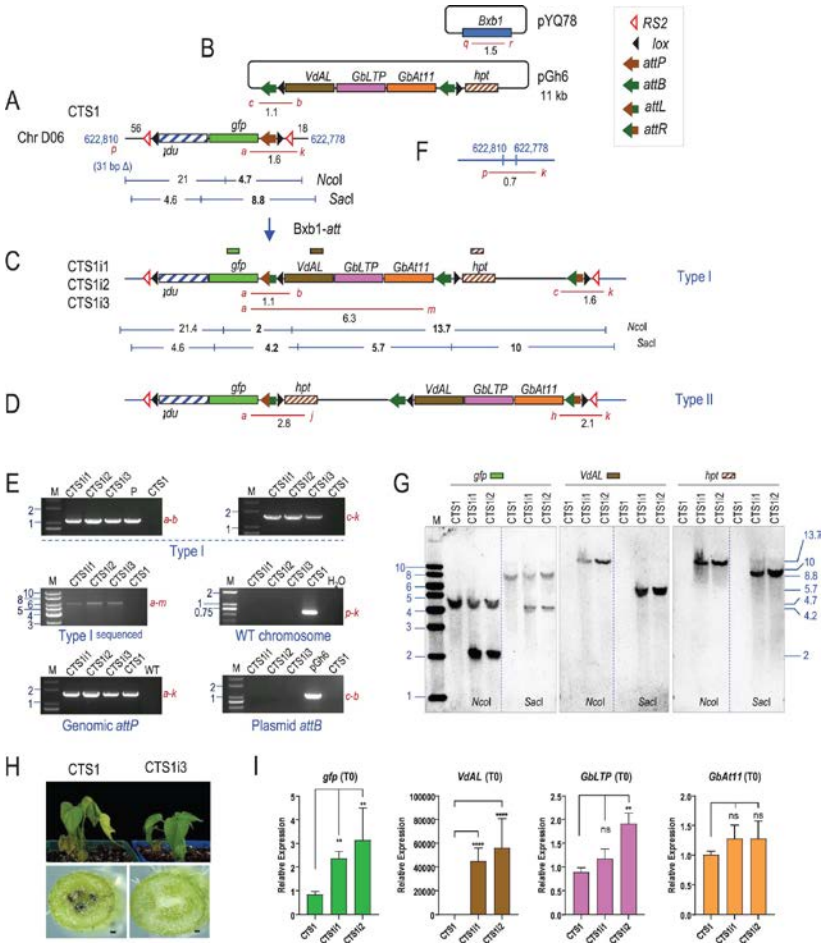


图1、A、CTS1中的基因组attP位点与pGh6（B）中的attB位点之间的重组，以产生（C）I型或（D）II型整合结构，由来自共转化pYQ78的Bxb1酶实现整合。E、位点特异性重组连接、WT位点、基因组attP和质粒attB的PCR检测结果。F、CTS1插入的WT染色体位点。红线表示PCR产物。G、 植物CTS1和整合植物CTS1i1和CTS1i2的Southern印迹用NcoI或SacI酶切，并与探针gfp、VdAL或hpt杂交。限制性酶切位点和预期片段如（A）和（C）所示。H、多基因（*VDAL*、*GbLTP3*及*GbAt11*）聚合植物CTS1i3在接种“Vd991”分生孢子后16天显示出对黄萎菌的抗性，比例尺：0.01 mm。I、与CTS1相比，CTS1i1和CTS1i2中位点特异性整合的性状基因的表达。每个基因的转录水平与多毛毛癣菌组蛋白3基因标准化。数据以三个样本重复的平均值±SD表示。未配对t检验的显著差异（**P 50.01，***P50.0001，ns，无显著性）。M：标记泳道，以kb为单位的片段大小；P：pZH84和pGh6体外重组的阳性对照；WT：Coker 312 DNA。

Figure 1. CTS1 derived site-specific integrant plants. A, Recombination between the genomic attP site in CTS1

with attB site in pGh6 (B) to produce (C) type I or (D) type II integration structure, catalyzed by Bxb1 integrase from co-transformed pYQ78. E, Representative PCR detection of site-specific recombination junctions, WT site, genome attP, and plasmid attB. F, WT chromosome site of corresponding CTS1 insertion. Red lines represent PCR products. G, Southern blots of plant CTS1 and integrant plants CTS1i1 and CTS1i2 cleaved with NcoI or SacI and hybridized with probe gfp, VdAL, or hpt. Restriction sites and expected fragments shown in (A) and (C). H, Integrated plant CTS1i3 showed resistance to Verticillium dahlia 16 d after inoculation with the “Vd991” conidial, scale bar: 0.01 mm. I, Expression of site-specifically integrated trait genes in CTS1i1 and CTS1i2 compared to CTS1. Transcript level of each gene normalized to G. hirsutum histone 3 gene. Data presented as means ± SD of three sample repeats. Significant differences according to unpaired t test (**P 50.01, ****P50.0001, ns, not significant). M: marker lane, fragment sizes in kb; P: positive control from pZH84 and pGh6 in vitro recombination; WT: Coker 312 DNA.

（二） 研究成果

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

Y Li，R Li，Z Han，H Wang，S Zhou，Y Li，Y Wang，J Qi，DW Ow (2022) Ow D. Recombinase-mediated gene stacking in cotton. ***Plant Physio*** 28;188 (4) : 1852-1865.

获奖：

三农金桥奖项目优秀奖（一等），大丽轮枝孢激活蛋白（VDAL）的研究与应用，中国技术市场协会。（**齐俊生，巩志忠**等，2022.11）

（三） 研究队伍

固定人员：

齐俊生（课题组长）。

研究生：

赵雯莉，李瑞，刘韵真，杨国华，李运芝，林如玉。

赖锦盛 课题组

赖锦盛，教授。

研究方向：玉米基因组学、玉米育种技术玉米分子育种。

（一） 研究进展

1、新型糖转运蛋白 SUGCAR1 在玉米籽粒灌浆过程中的作用

营养物质（光合产物和矿质养分）从母体组织向种子转移是影响籽粒发育和产量性状的关键因素。叶片光合作用产生的蔗糖通过韧皮部的长距离运输到达籽粒附近的母体组织，然后经由特殊组织转运进入籽粒。在玉米、高粱等谷类作物中，这种籽粒基部细胞分化、发育而成的特殊组织称为胚乳基底转移层 BETL（Basal Endosperm Transfer Layer）。研究表明，籽粒灌浆过程中部分蔗糖（双糖）先水解成单糖（葡萄糖和果糖），然后通过 BETL 的单糖转运体进入胚乳。另一种学说认为蔗糖也可以不水解而直接通过 BETL 进入胚乳。然而迄今为止，尚未在 BETL 中发现支持该学说的蔗糖转运体。该研究通过正向遗传学的方法筛选到一个玉米籽粒灌浆缺陷的突变体，通过图位克隆和 CRISPR/Cas9 技术验证，确定了玉米 *ZmNPF7.9*/*ZmSUGCAR1* 基因突变是导致籽粒灌浆缺陷表型的原因。*ZmSUGCAR1* 基因特异在玉米籽粒胚乳基底转移层（BETL）中表达。通过系统进化分析，发现 ZmSUGCAR1 是拟南芥 AtNPF7.3 的旁系同源蛋白。以往的研究表明，AtNPF7.3 具有钾离子转运活性，并参与拟南芥中钾离子和硝酸根离子的协同运输。本研究发现 *ZmSUGCAR1* 的功能缺失导致玉米籽粒中蔗糖和葡萄糖含量显著降低，进而导致籽粒皱缩的表型，同时籽粒中钾离子含量也显著降低。进一步利用非洲爪蟾卵母细胞和 HEK293T 细胞两种异源表达体系，通过同位素标记、双电极电压钳、膜片钳、离子流速测定等技术对 ZmSUGCAR1 蛋白的转运活性进行检测，发现 ZmSUGCAR1 不仅可以转运钾离子，令人意外的是 ZmSUGCAR1 还能够直接转运蔗糖和葡萄糖。ZmSUGCAR1 的糖转运活性依赖于跨细胞质膜的 pH 梯度，说明它是一个 H^+/糖耦联的同向转运体。值得注意的是，*ZmSUGCAR1* 在高粱和小麦中的直系同源基因 *SbSUGCAR1* 和 *TaSUGCAR1* 都在籽粒灌浆阶段特异表达，并且这两个蛋白同样具有蔗糖和葡萄糖的转运活性，表明 SUGCAR1 在谷类作物中的功能具有保守性，它们可能都参与籽粒灌浆过程（Yang et al., *Plant Cell*, 2022）。

The Sugar Transporter ZmSUGCAR1 of the Nitrate Transporter 1/Peptide Transporter Family is Critical for Maize Grain Filling

Maternal-to-filial nutrition transfer is central to grain development and yield. nitrate transporter 1/peptide transporter (NRT1-PTR) -type transporters typically transport nitrate, peptides, and ions. Here, we report the identification of a maize (*Zea mays*) NRT1-PTR-type transporter that transports sucrose and glucose. The activity of this sugar transporter, named Sucrose and Glucose Carrier 1 (*SUGCAR1*), was systematically verified by tracer-labeled sugar uptake and serial electrophysiological studies including two-electrode voltage-clamp, non-invasive microelectrode ion flux estimation assays in *Xenopus laevis* oocytes and patch clamping in HEK293T cells. *ZmSUGCAR1* is specifically expressed in the basal endosperm transfer layer and loss-of-function mutation of *ZmSUGCAR1* caused significantly decreased sucrose and glucose contents and subsequent shrinkage of maize kernels. Notably, the *ZmSUGCAR1* orthologs *SbSUGCAR1* (from *Sorghum bicolor*) and *TaSUGCAR1* (from *Triticum aestivum*) displayed similar sugar transport activities in oocytes, supporting the functional conservation of SUGCAR1 in closely related cereal species. Thus, the discovery of ZmSUGCAR1 uncovers a type of sugar transporter essential for grain development and opens potential avenues for genetic improvement of seed-filling and yield in maize and other grain crops (Yang et al., *Plant Cell*, 2022).

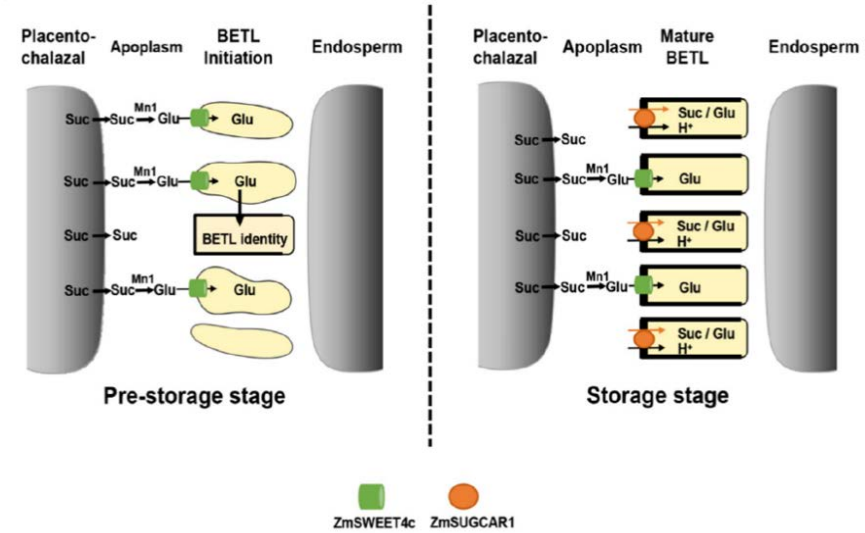


图 1、ZmSUGCAR1 转运蔗糖调控玉米籽粒灌浆。

Figure 1. A shematic model of ZmSUGCAR1 in regulating grain filling in maize.

2、利用 CRISPR type I 系统实现基因组靶向大片段删除

目前 CRISPR-Cas 系统已被广泛用于动植物的基因组编辑，其中来自于 type II 型的 Cas9 系统可以实现基因组的插入、敲除、单碱基编辑等。然而目前对于大片段缺失工具的研究相对较少且效

率低下。尽管研究表明 type I-E 系统可以诱导基因组单向的大片段删除。然而，其精确性有待被进一步优化。在此，我们开发了一个紧凑的 Dvu I-C 系统，并证实了含有 Cas11c 的 Dvu I-C 系统可以用于植物基因组编辑（图 2）。通过使用双 crRNA 的设计，我们发现 Dvu I-C 系统使用成对的 crRNA 可以有效地引入了可控制的大片段删除，最少可达 20 kb。并且这种设计也可用于提高 type I-E 系统的删除可控性。通过对不同间隔长度和错配的耐受度分析，我们证实了 Dvu I-C 系统对错配敏感，有利于提高编辑的特异性。此外，我们还发现 Dvu I-C 系统可以有效地在玉米和水稻中生成稳定的转基因株系，编辑效率可达 86.7%。该研究开发了可以高效应用于基因组大片段缺失的基因编辑工具-Dvu I-C，进一步丰富了基因编辑工具的多样性。

Targeted Large Fragment Deletion in Plants using Paired crRNAs with Type I CRISPR Systems

At present, CRISPR-Cas system has been widely used in genome editing of plants and animals, CRISPR-Cas9 system from type II can achieve genome knock-in, knockout, base editing. However, the research on large fragment deletion tools is relatively few and inefficient. Although some studies have shown that the type I-E system can induce large fragment deletion with unidirectional segments deletion on human genome. The accuracy needs to be further optimized. Here, we develop a compact Dvu I-C system and confirm that Dvu I-C system with Cas11c can be used for plant genome editing (Figure 2). By using a dual crRNA design, we found that the Dvu I-C system using paired crRNAs effectively introduced controlled large fragment deletion at least up to 20 kb. It can also be used to improve the controllability of deletion in type I-E systems by using paired crRNAs. By analyzing the tolerance of different spacer lengths and mismatches, we confirmed that the Dvu I-C system is sensitive to mismatches. which is conducive to improving the specificity of editing. In addition, we found that the Dvu I-C system can effectively generate stable transgenic lines in maize and rice, with editing efficiency up to 86.7%. This research has enriched the existing genome editing system and developed a genome editing tool, Dvu I-C, which can be effectively applied to large fragment deletion.

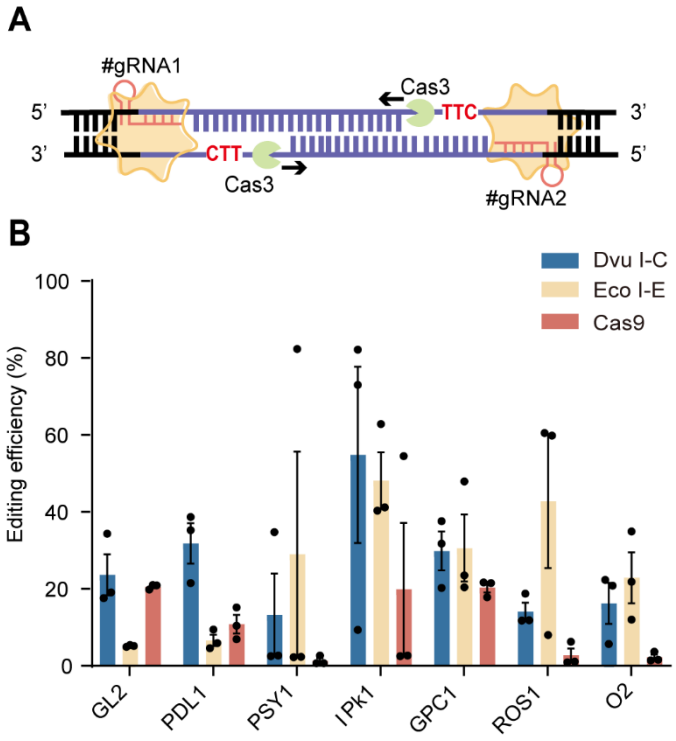


图 2、Type I CRISPR 系统介导的大片段缺失效率。

Figure 2. Editing efficiency of targeted large ragment deletion introduced by Type I CRISPR Systems.

3、利用三代测序技术绘制玉米自交系的基因组结构图谱

在玉米驯化和改良过程中，基因组结构变异对基因组和表型的多样性起了至关重要的作用。由于玉米基因组的高复杂度，绘制群体水平的基因组结构变异图谱极具挑战。在此研究中，我们利用三代测序技术，精准调试了适合玉米基因组的碱基识别模型，开发了鉴定结构变异的算法。在 100 多个重要的玉米自交系和祖先种大刍草中，我们共鉴定到了 245,277 个缺失和 156,642 个插入。首先，由每个自交系的结构变异集合定义的自交系间的进化距离，重现了自交系群体内部的进化关系。同时，每个自交系的结构变异集合也展示了大量新的 IBS 区域和基因渗入事件。其次，将近 80%的群体水平的结构变异和转座子同时出现，而 Gypsy 转座子介导的结构变异在中心体周围和染色体端粒附近最为富集。第三，由 DNA/T 和 MITEs 类型的转座子介导的结构变异比由 LTR 元件介导的结构变异更不容易在群体中被保留下来。此外，除了 DNA/T 和 MITE 介导的缺失外，大部分的结构变异是有害的，原因是这两种类型的转座子插入时间相对老。第四，在基因表达的层面，全基因组有上千个结构变异能显著地顺式调控附近基因的表达。本研究绘制的玉米自交系群体的基因组结构图谱，为研究玉米驯化过程中的结构变异提供了很好的资源，并有望指导玉米重要农艺性状的改良。

Mapping Genome-wide Structural Variations of 106 Maize Lines with Nanopore Sequencing

Structural variations (SVs) contribute substantially to maize genome diversity and phenotype variability during domestication and improvement. Due to the high complexity of maize genome, a population-level SV catalog remains challenging. Here we utilized the long-read nanopore sequencing, curated base calling and SV discovery algorithms, and identified 245,277 deletions and 156,642 insertions in more than 100 maize and teosinte lines. The per-accession SV sets reiterate major evolutionary context and reveal extensive identity-by-state (IBS) regions and gene introgression. Around 80% of the SVs colocalize with transposon elements, among which Gypsy drives most abundant SVs in both pericentromeric and telomeric regions. SVs driving by DNA/T and MITEs are less prone to be retained than LTR elements. Most SVs are deleterious except for the DNA/T and MITE-related deletions, which might be explained by their relatively old insertion time. Thousands of SVs mediate significantly different expression of nearby genes. Our results established a great resource for investigating SVs involving maize domestication and for guiding maize agronomic improvement.

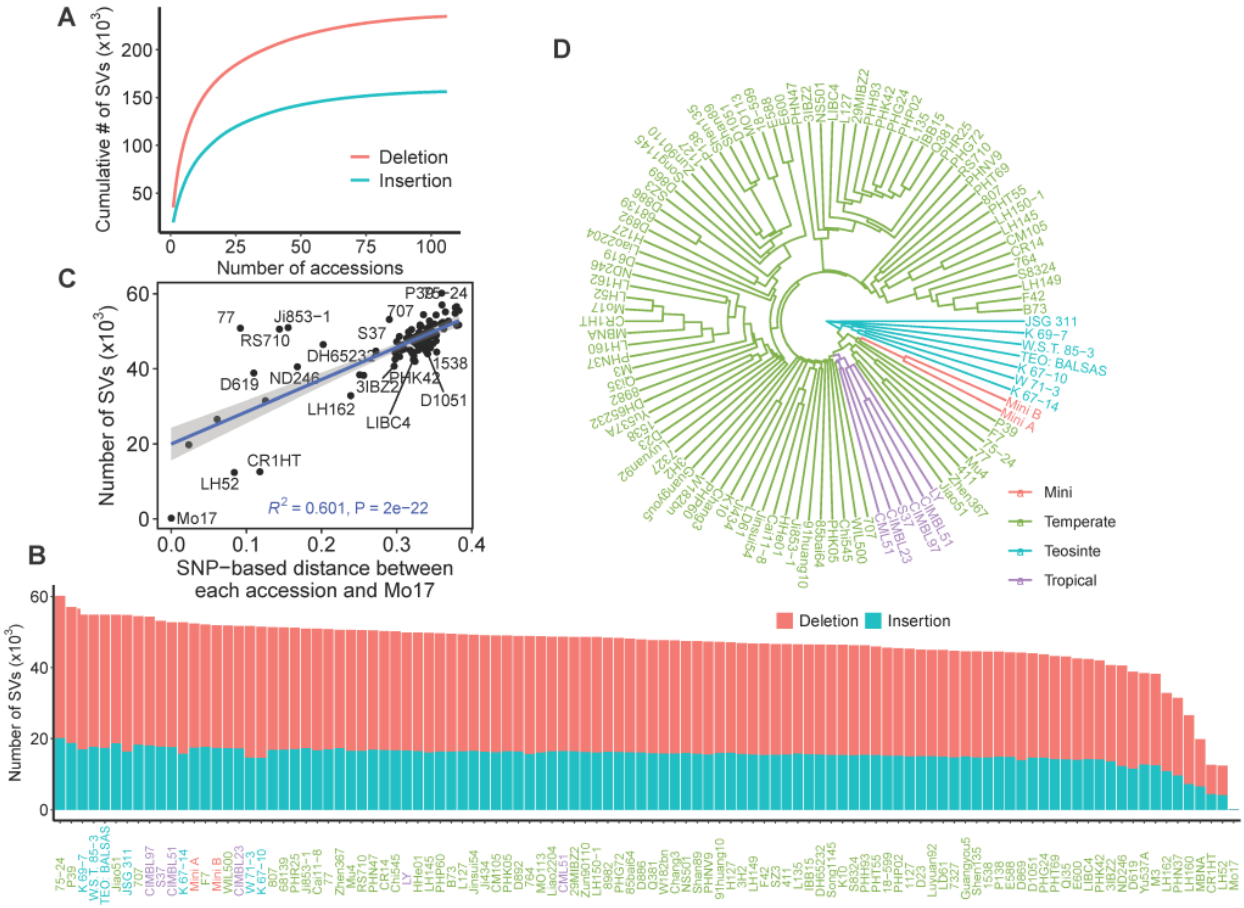


图 3、每个自交系结构变异的鉴定和评价。（A）SVCollector 曲线描述了随着自交系数量的增加，检测到的群体水平的插入和缺失的累计数量。增加的自交系的顺序用的是“贪婪”算法。（B）鉴定到的每个自交系在插入和缺失的数量分布。一般而言，插入少于缺失。（C）散点图展示了每个自交系的结构变异的数量和自交系与 Mo17 之间距离的关系。

（D）基于该自交系群体的结构变异的 PAV 矩阵聚类，展示了自交系间的进化关系。图中 4 个子群体的颜色和图（B）中的子群体颜色对应。

Figure 3. per-accession SV discovery and its evaluation. (A) SVCollector curves of cumulative insertions and deletions identified in 106 accessions. The order of added accessions was determined by “greedy” algorithm. (B) The distribution of the number of per-accession deletions and insertions. Generally, less insertions were identified than deletions. (C) The scatterplot shows the correlation between the number of per-accession SVs and the SNP-based distance between each accession and Mo17. (D) The clustering of SV presence/absence matrix for 106 maize accessions. The colors for maize subpopulations match the colors in (B).

4、玉米穗行数新 QTL 的鉴定

本研究使用了一个新的玉米 NAM 群体—HNAU-NAM1，共 1617 个重组自交系，共同亲本为玉米自交系 GEMS41，在 4 种环境下对群体材料的穗行数进行考察。然后，利用联合连锁映射（joint linkage mapping，JLM）方法在至少 3 种环境中识别出分布在 4 条染色体上的 5 个稳定的 QTLs；通过分离连锁映射（SLM）和全基因组关联研究（GWAS）方法进一步验证了这些 QTLs。这 5 个 QTL 有 3 个 QTL 的功能基因已经被鉴定并做了验证，包括 qKRN1.1、qKRN2.1 和 qKRN4.1。同时还发现了两个新的穗行数 QTLs，qKRN4.2 和 qKRN9.1。根据公共 RNA-seq 和基因组注释数据，5 个在幼穗中高表达的基因被认为可能是调控穗行数的候选基因（Fei et al., *BMC Genomics,* 2022）。

Identification of Two New QTLs of Maize (Zea Mays L.) Underlying Kernel Row Number Using the HNAU-NAM1 Population

Here, we measured KRN in four environments using a nested association mapping (NAM) population named HNAU-NAM1 with 1,617 recombinant inbred lines (RILs) that were derived from 12 maize inbred lines with a common parent, GEMS41. Then, five consensus quantitative trait loci (QTLs) distributing on four chromosomes were identified in at least three environments along with the best linear unbiased prediction (BLUP) values by the joint linkage mapping (JLM) method. These QTLs were further validated by the separate linkage mapping (SLM) and genome-wide association study (GWAS) methods. Three KRN genes cloned through the QTL assay were found in three of the five consensus QTLs, including qKRN1.1, qKRN2.1 and qKRN4.1. Two new QTLs of KRN, qKRN4.2 and qKRN9.1, were also identified. On the basis of public RNA-seq and genome annotation data, five genes highly expressed in ear tissue were considered candidate genes contributing to KRN (Fei et al., *BMC Genomics,* 2022).

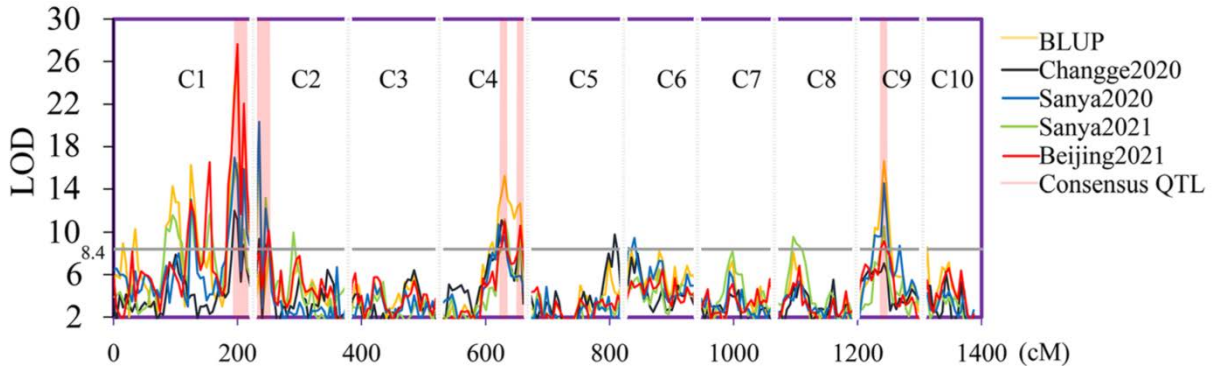


图 4、不同环境下利用 HNAU-NAM1 群体定位的穗行数 QTL。

Figure 4. QTLs associated with KRN under different environments in the HNAU-NAM1 population.

5、玉米授粉前后胚囊高时间分辨率转录组图谱绘制

玉米籽粒的发育起始于发生在胚囊内的双受精过程，在该过程中两个精细胞分别与卵细胞和中央细胞发生融合，形成合子和受精极核。在籽粒的早期发育过程中合子和受精极核都需要经历一系列动态的生物学过程才能发育分化形成胚和胚乳。尽管玉米籽粒被广泛应用于食品、饲料和生物燃料等方面，但是目前玉米籽粒转录组研究主要集中于籽粒发育的中后期，而针对籽粒早期生长发育过程中基因的表达模式和调控机制的研究相对缺乏。本研究通过对授粉后0-4天内的44个发育时间点的胚囊和去掉胚囊的胚珠进行了取样和转录组测序，系统地绘制了胚囊和胚珠的高时间分辨率转录组图谱。我们在授粉后0-4天内的胚囊和去掉胚囊的胚珠中共鉴定到25,187个基因表达，其中包括1,598个转录因子。通过对这些基因的表达模式进行归类分析，我们将玉米籽粒的早期发育过程划分成5个阶段：双受精、合子的有丝分裂和不对称分裂以及胚乳的多核体、细胞化和细胞分化阶段。此外，共鉴定到3,327个籽粒特异表达基因，其中有1,145个基因是本研究新鉴定到的。这些基因中有859个主要在胚囊中特异表达，186个主要在胚珠中特异表达。我们还结合本实验室已发表的玉米籽粒转录组数据，分析了参与生长素合成、转运和信号转导等一系列过程的基因在籽粒发育过程中不同时期不同组分间的表达模式。研究结果将有助于进一步解析玉米籽粒早期发育的发育进程和分子调控机制，为玉米籽粒性状改良提供新的基因组学资源（Li et al., *Plant Mol Biol*, 2022）。

High Temporal-Resolution Transcriptome Landscapes of Maize Embryo sac and Ovule during Early Seed Development

The early maize (*Zea mays*) seed development is initiated from double fertilization in the embryo sac and needs to undergo a highly dynamic and complex development process to form the differentiated embryo and endosperm. Despite the importance of maize seed for food, feed, and biofuel, many regulators responsible for controlling its early development are not known yet. Here, we reported a high temporal-resolution transcriptome atlas of embryo sac and ovule based on 44 time point samples collected within the first four days of seed development. A total of 25,187 genes including 1,598 transcription factors (TFs) involved in early seed development were

detected. Global comparisons of the expressions of these genes revealed five distinct development stages of early seed, which are mainly related to double fertilization, asymmetric cell division of the zygote, as well as coenocyte formation, cellularization and differentiation in endosperm. We identified 3,327 seed-specific genes, which more than one thousand seed-specific genes with main expressions during early seed development were newly identified here, including 859 and 186 genes predominantly expressed in the embryo sac and ovule, respectively. Combined with the published transcriptome data of seed, we uncovered the dominant auxin biosynthesis, transport and signaling related genes at different development stages and subregions of seed. These results are helpful for understanding the genetic control of early seed development (Li et al., *Plant Mol Biol*, 2022).

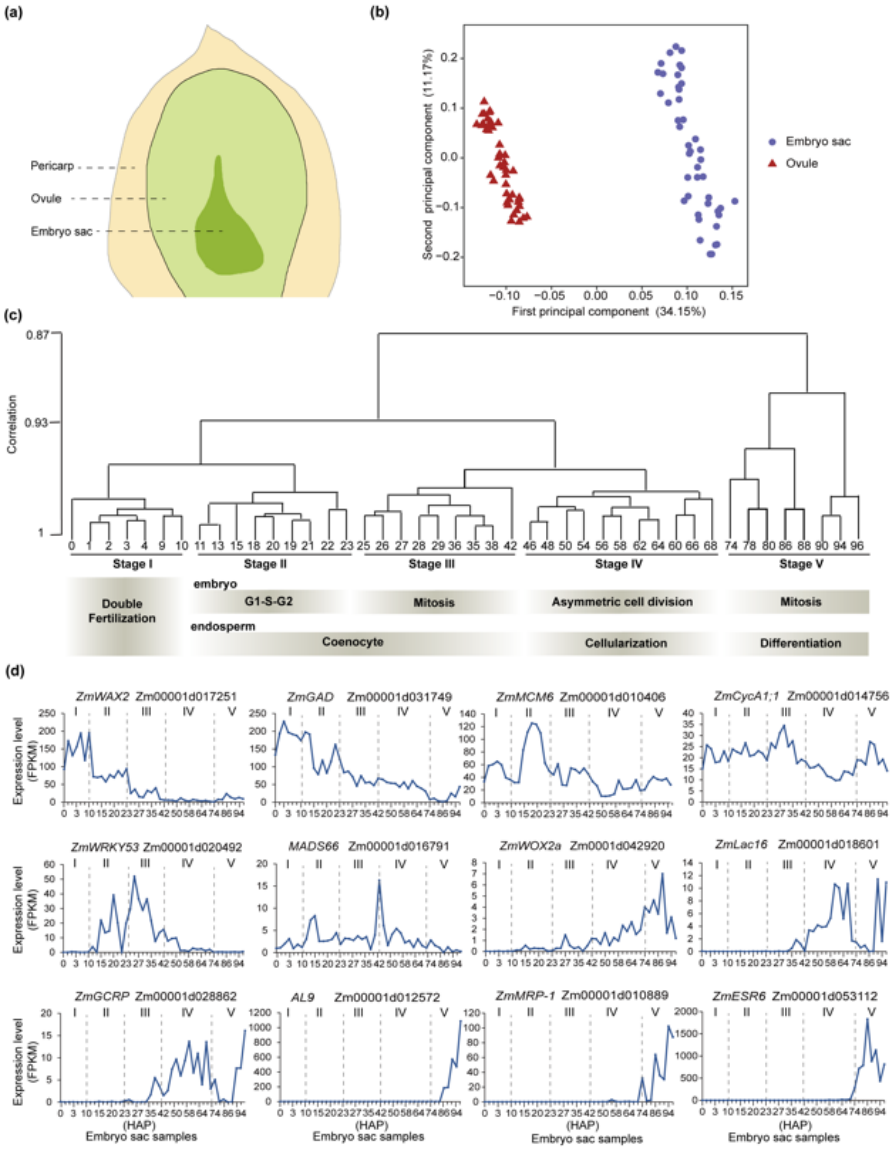


图5、籽粒发育早期44个时间点胚囊和胚珠间的转录组关系。

Figure 5. Transcriptome relationships among 44 time points of embryosac and ovule samples during early seed development.

（二） 研究成果

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

1. Yang B, Wang J, Yu M, Zhang M, Zhong Y, Wang T, Liu P, Song W, Zhao H, Fastner A, Suter M, Rentsch D, Ludewig U, Jin W, Geiger D, Hedrich R, Braun D. M, Koch K. E, McCarty D. R, Wu W. H, Li X*, **Wang Y* and Lai J*** (2022) The sugar transporter ZmSUGCAR1 of the Nitrate Transporter 1/Peptide Transporter family is critical for maize grain filling. ***Plant Cell*** 34: 4232-4254.
2. Fei X, Wang Y, Zheng Y, Shen X, E L, Ding J, Lai J, **Song W*, Zhao H*** (2022) Identification of two new QTLs of maize (*Zea mays L*.) underlying kernel row number using the HNAU-NAM1 population. ***BMC Genomics*** 23:593.
3. Li X#, Wu J#, Yi F#, **Lai J, Chen J*** (2022) High temporal-resolution transcriptome landscapes of maize embryo sac and ovule during early seed development. ***Plant Mol Biol*** Accepted.

（三） 研究队伍

固定人员：

赖锦盛（课题组长），宋伟彬，赵海铭，鄂立柱，辛蓓蓓，陈建。

博士后：

李建锐，张美玲，申晓蒙，李元，刘胜男，张莉莉，徐峰，李卓洋。

研究生：

李英男，李元，李鑫晨，王莹莹，岳阳，黄亮亮，徐江海，王子健，林臻，吕梦璐，唐努尔·卡德尔别克，谭凯文，王乙霏，陆琼，杨静，周跃恒，李英双，洪祥德，白雨禾，刘天翔，李可，卿香玉，邓伟，邓喜真，龚慧慧，刘蕤丹，罗紫薇，余镁霞，王冠峰，李枳蒙，郑云霄，马萌，赵子龙，崔光辉，赵宇欣，李盈佳，郭冰，黄曼清，李佳琪，张政权，蔡铭铭，朱仁钊，张馨月，梁志颖，代亚方，孔珂，曹旭杰，滕云鹏，高亚兰，易欣，李沛洋，石志康，屈卫星，彭晨晨，王悦，曹剑。

金危危

课题组

金危危，教授。

研究方向：作物基因组学。

（一） 研究进展

1、热激蛋白 HSP101 调控玉米花粉母细胞减数分裂抗热性

减数分裂是植物有性生殖的关键环节，虽然研究表明高温会影响植物减数分裂重组以及后续的减数分裂进程，但调控减数分裂抗热性的基因鲜有报道。本研究以一个玉米经典的显性雄性不育突变体 *Ms42* 为研究对象。细胞学观察发现，*Ms42* 突变体花粉母细胞减数分裂前期 I 的同源染色体配对和联会存在缺陷，减数分裂的 DNA 双链断裂修复也有异常。通过基因图位克隆发现，*Ms42* 编码热激蛋白 HSP101，主要在花粉母细胞中表达。利用基因编辑技术获得 *hsp101* 的无效突变体，该突变体常温下减数分裂和育性没有显著异常；但经过短暂高温处理后，*hsp101* 突变体中 DSB 修复关键蛋白 RAD51 不能被招募到减数分裂染色体上，后续减数分裂过程也出现显著异常。与之对应地，过表达 *HSP101* 显著增强小孢子发育的抗热性。综上所述，HSP101 调控玉米小孢子发育的抗热性，该研究为玉米雄性减数分裂高温适应性的遗传机理提供了新的见解（Li et al., *Plant Cell*, 2022）。

Heat Shock Protein 101 Contributes to the Thermotolerance of Male Meiosis in Maize

High temperatures interfere with meiotic recombination and the subsequent progression of meiosis in plants, but few genes involved in meiotic thermotolerance have been characterized. Here, we characterize a maize (*Zea mays*) classic dominant male-sterile mutant *Ms42*, which has defects in pairing and synapsis of homologous chromosomes and DNA double strand break (DSB) repair. *Ms42* encodes a member of the heat shock protein family, HSP101, which accumulates in pollen mother cells. Analysis of the dominant *Ms42* mutant and *hsp101* null mutants reveals that HSP101 functions inRADIATION SENSITIVE 51 loading, DSB repair, and subsequent meiosis. Consistent with these functions, overexpression of *Hsp101* in anthers results in robust microspores with enhanced heat tolerance. These results demonstrate that HSP101 mediates thermotolerance during microsporogenesis, shedding light on the genetic basis underlying the adaptation of malemeiocytes to high temperatures (Li et al., *Plant Cell*, 2022).

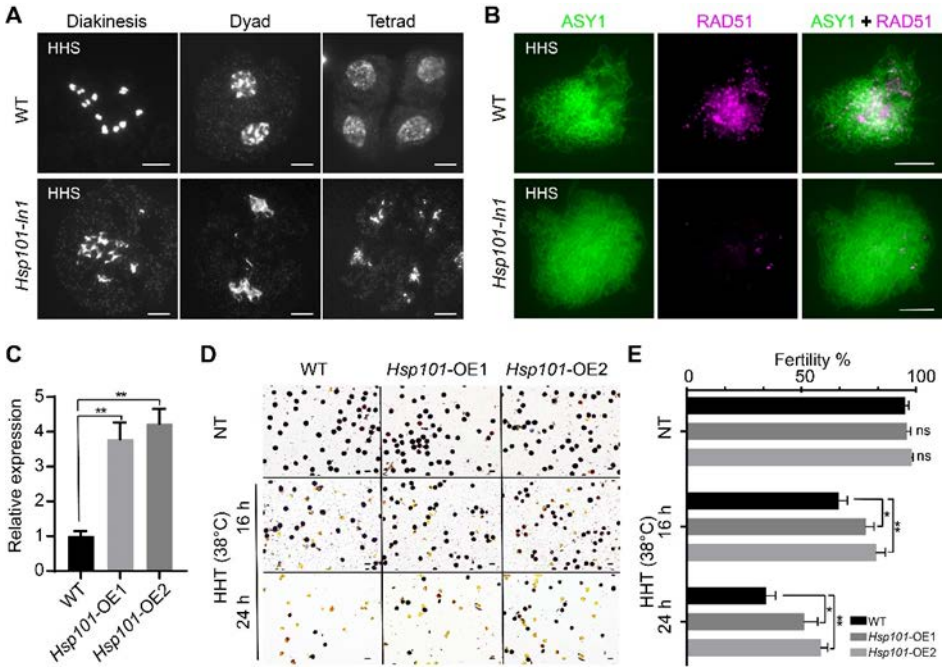


图 1、HSP101 调控玉米花粉母细胞减数分裂的抗热性。

Figure 1. HSP101 mediates thermotolerance of pollen mother cells in maize.

2、细胞质转化酶 INVAN6 调控玉米减数分裂过程

减数分裂过程对可育配子的产生十分必要，过去的研究表明植物雄性减数分裂对环境温度较为敏感，但相关分子机制仍不够清晰。该研究以一个玉米显性雄性不育突变体 *Mei025* 为研究对象。*Mei025* 突变体的花粉母细胞在粗线期之后发生减数分裂停滞，从而导致花粉败育。通过基因图位克隆发现，*Mei025* 突变体中编码细胞质转化酶 INVAN6 的基因上发生了一个点突变，导致 INVAN6 第 276 位天冬氨酸被替换成了天冬酰胺。INVAN6 特异性地水解蔗糖，主要在花粉母细胞中富集。INVAN6 能自身互作，还能和其它四个细胞质转化酶以及七个 14-3-3 蛋白互作。突变型的 INVAN6^{Mei025} 蛋白虽然没有蔗糖水解酶活性，但它的存在会导致减数分裂异常，可能通过显性负效应的方式干扰了野生型 INVAN6 或其同源蛋白以及互作蛋白的功能。通过基因编辑技术获得了 *invan6* 的无效突变体，热胁迫下发生减数分裂异常；进一步的转录组分析结果表明，INVAN6 对于雄性减数分裂的糖分稳态和抗逆性有重要作用。综上所述，该研究发现一个细胞质转化酶 INVAN6 参与热胁迫下的糖代谢和糖信号调控，从而保障减数分裂的正常进行（Huang et al., *New Phytol*, 2022）。

Maize Cytosolic Invertase INVAN6 Ensures Faithful Meiotic Progression Under Heat Stress

Faithful meiotic progression ensures the generation of viable gametes. Studies suggested the male meiosis of plants is sensitive to ambient temperature, but the underlying molecular mechanisms remain elusive. Here we characterized a maize dominant male sterile mutant *Mei025*,

in which the meiotic process of pollen mother cells (PMCs) was arrested after pachytene. An Asp-to-Asn replacement at position 276 of INVERTASE ALKALINE NEUTRAL 6 (INVAN6), a cytosolic invertase (CIN) predominantly exists in PMCs and specifically hydrolyses sucrose, was revealed to cause meiotic defects in *Mei025*. INVAN6 interacts with itself as well as with four other CINs and seven 14-3-3 proteins. Although INVAN6^{Mei025}, the variant of INVAN6 found in *Mei025*, lacks hydrolytic activity entirely, its presence is deleterious to male meiosis, possibly in a dominant negative repression manner through interacting with its partner proteins. Notably, heat stress aggravated meiotic defects in *invan6* null mutant. Further transcriptome data suggests INVAN6 has a fundamental role for sugar homeostasis and stress tolerance of male meiocytes. In summary, this work uncovered the function of maize CIN in male meiosis and revealed the role of CIN-mediated sugar metabolism and signalling in meiotic progression under heat stress.

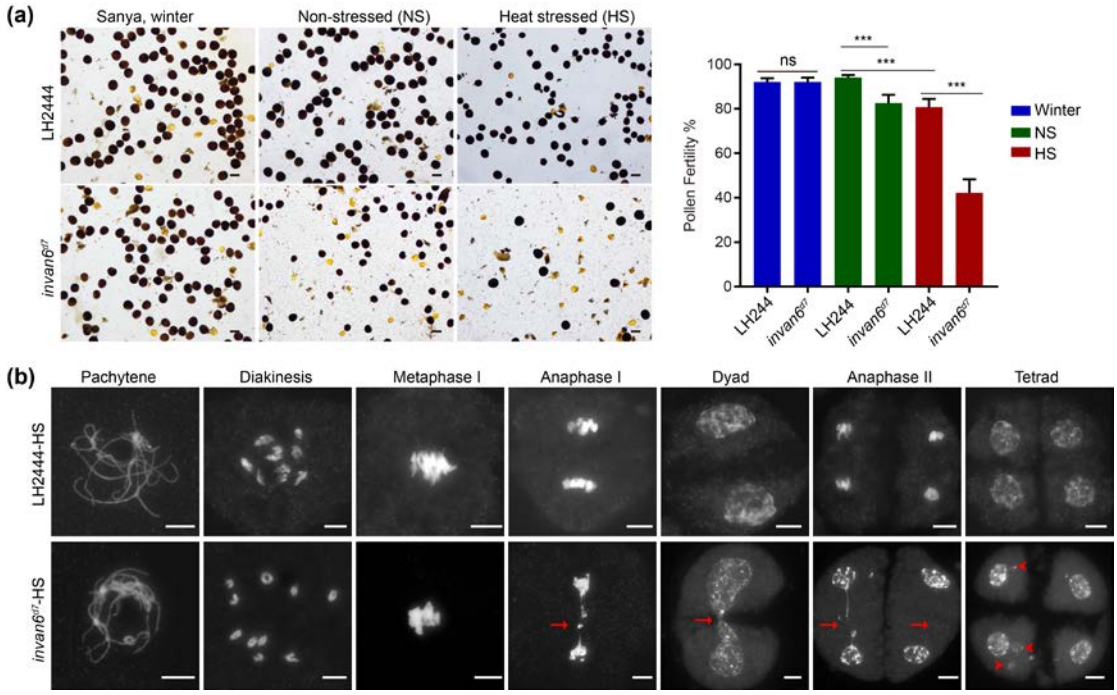


图 2、细胞质转化酶 INVAN6 调控玉米减数分裂过程的抗热性。

Figure 2. INVAN6 mediates thermotolerance of maize male meiosis.

（二） 研究成果

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

1. Li Y, Huang Y, Sun H, Wang T, Ru W, Pan L, Zhao X, Dong Z, Huang W*, **Jin W*** (2022) Heat shock protein 101 contributes to the thermotolerance of male meiosis in maize. ***Plant Cell*** 34: 3702-3717.
2. Huang W#, Li Y#, Du Y, Pan L, Huang Y, Liu H, Zhao Y, Shi Y, Ruan YL, Dong Z*, **Jin W*** (2022) Maize cytosolic invertase INVAN6 ensures faithful meiotic progression under heat

stress. ***New phytol*** 236: 2172-2188.

3. Wang T, Li Y, Huang Y, Zhao X, Dong Z, **Jin W***, Huang W* (2022) Amino acid permease 6 regulates grain protein content in maize. ***Crop J*** 10: 1536-1544.
4. Meng D#, Luo H#, Dong Z, Huang W, Liu F, Li F, Chen S, Yu H*, **Jin W*** (2022) Overexpression of Modified CENH3 in Maize Stock6-Derived Inducer Lines Can Effectively Improve Maternal Haploid Induction Rates. ***Front Plant Sci*** 13: 892055.

专利申请：

1. 蛋白质 INVAN6、其编码基因以及它们在选育玉米雄性不育系中的应用。申请人：**金危危**，黄伟，李云飞；专利号：ZL201910387858.0；授权日期：2022 年 08 月 09 日。
2. 蛋白质 HEI10 在调控玉米产量和抗病性中的应用。申请人：**金危危**，**王喜庆**，李云飞*，赵晓明，黄伟，庄军红，潘玲玲；专利号：ZL201910602376.2；授权日期：2022 年 04 月 05 日。

（三） 研究队伍

固定人员：

金危危（课题组长），黄伟。

研究生：

孙丰坤，王雅鑫，茹玮，潘玲玲，苏晗，辛志奇，姜正博，匡英铭，郑登科，付玉，蔡林鑫，张艳，吴一迪。

徐明良

课题组

徐明良，教授。

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、玉米灰斑病抗病基因的发掘和抗病机理解析

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，玉米灰斑病业已成为继玉米大、小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。我们课题组前期检测到了两个主效 QTL，*qRgls1* 和 *qRgls2*，分别位于玉米第 8 和第 5 号染色体上。通过多年的精细定位，分别将它们限定在 60kb 和 80kb 的区间内。经转基因功能验证，证实 *ZmWAKL* 和 *ZmCDPK* 为这两个位点的抗病基因，并对这两个基因的抗病机理进行了初步探究。

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。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。

另一个抗病基因 *ZmCDPK* 编码的钙依赖蛋白激酶，磷酸化下游靶标 ZmDi19 第 117 位丝氨酸，促使转录因子 ZmDi19 的降解，进而负调控玉米对灰斑病的抗性。转基因功能验证确认 *ZmDi19* 正调控灰斑病抗性。结合转录组和蛋白组结果，并通过酵母单杂交和表达分析鉴定到 ZmDi19 调控的靶标基因 *ZmPR10*，且过表达 *ZmPR10* 显著增强了玉米对灰斑病的抗性。

Identification and Characterization of Two Major QTL 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 and Southern corn leaf blight, which causes 5-30% yield loss every year. When severely infected, the disease causes plant death, resulting in complete yield loss. We previously detected two major QTL, designated *qRgls1* and *qRgls2*, located on chromosomes 8 and 5, respectively. Thereafter, we delimited *qRgls1* and *qRgls2* into 60kb and 80kb intervals, respectively, by a sequential fine-mapping strategy. Transgenic validation demonstrated that *ZmWAKL* and *ZmCDPK* are the genes within *qRgls1* and *qRgls2* conferring resistance to GLS.

ZmWAKL encodes a cell wall-associated receptor-like kinase, which can bind to its co-receptor ZmWIK on the plasma membrane and enhance each other's phosphorylation level. ZmWAKL/ZmWIK immune complex can bind to a receptor-like cytoplasmic kinase ZmBLK1 and transmit phosphorylation signal. The activated ZmBLK1 directly binds to 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.

Another resistance gene *ZmCDPK* encodes a calcium-dependent protein kinase, which phosphorylates a downstream target ZmDi19 on its Ser-117 to negatively regulate the stability of ZmDi19 protein, leading to susceptibility to maize gray leaf spot. Transgenic functional test confirmed that ZmDi19 positively regulates GLS resistance. Combining transcriptome and proteome data, yeast-to-hybridization and transient expression analysis, we identified *ZmPR10*, a target gene regulated by ZmDi19 and overexpression of *ZmPR10* significantly enhanced maize resistance to gray spot.

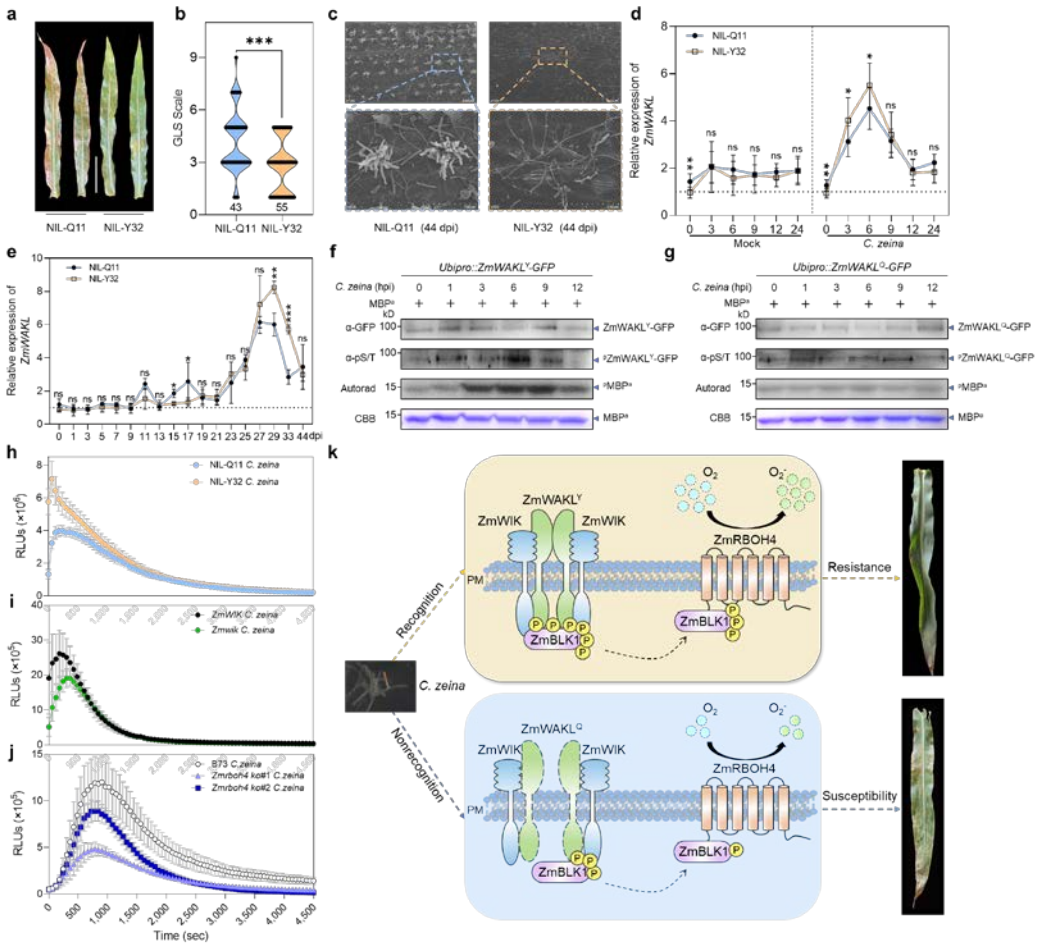


图 1、ZmWAKL 介导的免疫反应和分子模型。

Figure 1. The ZmWAKL-triggered immune response to *C. zeina* and proposed working model.

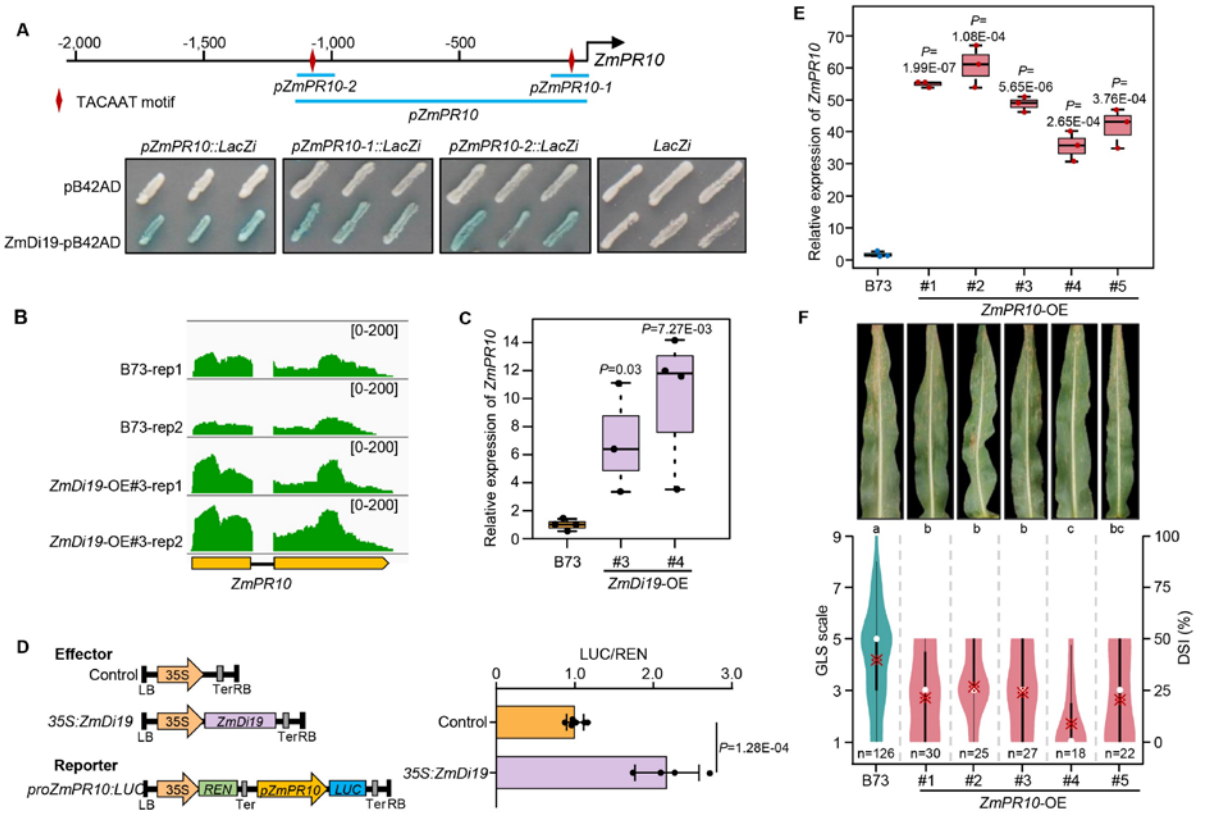


图 2、ZmDi19 正调控 *ZmPR10* 的表达和灰斑病抗性。

Figure 2. ZmDi19 activates the gene expression of *ZmPR10* to positively regulate GLS resistance.

2、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的挖掘：本年度针对前期鉴定到的主效 QTL-*qRfg3*，我们通过加密分子标记进一步精细定位，并最终将 *qRfg3* 定位到分子标记 M30 和 M13 之间约 10kb 的区段内。利用定位区段内的分子标记筛选抗、感材料的 BAC 文库，并最终构建了覆盖定位区段的 BAC 克隆重叠群。对覆盖定位区间的重叠 BAC 克隆测序，发现定位区间内长度为 4-kb 的拷贝数变异与茎腐病抗性高度相关。在定位区间附近有一个功能基因，命名为 *ZmBAG4*，抗、感等位基因之间存在 3 个 SNP 位点的差异，对 *ZmBAG4* 的突变体进行接种鉴定，初步验证了 *ZmBAG4* 的抗茎腐病功能。

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期。前期研究根据 *ZmCCT* 启动子序列变异将其划分为 15 种单倍型，经过表型鉴定发现抗病 *ZmCCT* 单倍型在长日照条件下具有光周期敏感性。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，经过筛选获得有代表性的 45 种编辑材料，并进行表型鉴定。本年度鉴定了 F_6 和 BC_2F_4 代 *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。综合鉴定结果，我们确定其中 2 种编辑类型材料综合表现较好，与抗病亲本相比，其开花期提前 15-20 天，而抗病性保持不变，且在两年间性状表现稳定。但相同编辑类型的不同重复之间存在差异，说明背景差异对表型影响较大，因此，准确获得导致开花期和抗病性改变的功能位点仍需进一步研究。

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 gain-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.

Discovery of new resistance locus against maize *Gibberella* stalk rot: For the previously identified QTL-*qRfg3*, we developed high-density molecular markers within the *qRfg3* region for further fine-mapping. We eventually mapped *qRfg3* to a 10-kb interval flanked by the molecular markers M30 and M13. The markers in the mapped region were used to screen two BAC libraries constructed from the resistant and susceptible inbred lines, and build two BAC contigs covering the final fine mapping region. Alignment of BAC sequences between two parental lines H127R and chang7-2 allowed us to identify a 4-kb length copy-number variation that was highly associated with stalk rot resistance. There is a functional gene near the mapped region, named *ZmBAG4*. Both resistant and susceptible *ZmBAG4* alleles are conserved in their sequences except for three SNPs. Inoculation on the null *ZmBAG4* mutant caused by *Mutator* insertion preliminarily revealed that *ZmBAG4* may be involved in maize resistance to *Gibberella* stalk rot.

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. The presence/absence of TE insertion and sequence variations at the *ZmCCT* promoter region allow us to identify at least 15 *ZmCCT* haplotypes, in which the resistance *H6* haplotype showed photoperiod sensitivity under long-day conditions. To reduce photoperiod sensitivity and keep the stalk-rot resistance, we used CRISPR/Cas9 to edit the promoter sequence, especially those photoperiod-responsive cis-elements. Totally, we got 45 different editing types to assess both disease resistance and photoperiod sensitivity. Of them, two exhibited desirable phenotypes in the field tests, with early flowering by 15-20 days and unchangeable disease resistance. However, great variations of the same editing type in different replicates indicate that genetic background may have a greater impact on phenotype. Thus far, the pivotal regulatory motifs of *ZmCCT* affecting flowering time and disease resistance need further investigation and analysis.

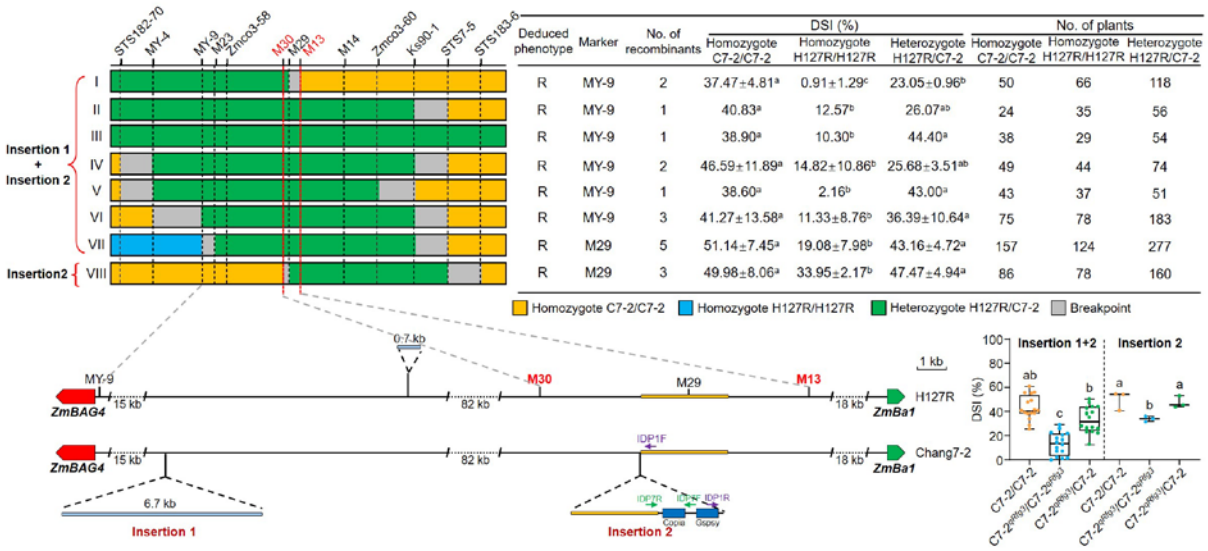


图 3、图位克隆 *qRfg3*。

Figure 3. Map-based cloning of *qRfg3*.

3、ZmGDIα-hel 调控玉米粗缩病隐性数量抗性的机理解析

粗缩病是世界玉米生产上广泛分布的一种病毒性病害，俗称玉米“癌症”。前期我们已证明 *ZmGDIα-hel* 是玉米粗缩病隐性数量抗性基因，且已验证寄主的 ZmGA2ox7.3 蛋白分别与感病蛋白 ZmGDIα、抗病蛋白 ZmGDIα-hel 和病毒蛋白 P7-1 互作。深入研究发现 ZmGA2ox7.3 与 ZmGDIα 的结合能力强于 ZmGDIα-hel。由感病蛋白形成的异源多聚体 ZmGA2ox7.3/ZmGDIα/P7-1 比相应的抗病蛋白形成的异源多聚体 ZmGA2ox7.3/ZmGDIα-hel/P7-1 可以显著提高 ZmGA2ox7.3 的双加氧酶活性，将有生物活性的内源赤霉素 GA_1/GA_4 转换成无生物活性的 GA_8/GA_{34}，从而极大干扰内源激素的稳态，进而引起节间缩短等粗缩病表型。

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

Maize rough dwarf disease (MRDD) is a predominant viral disease worldwide, known as ‘the cancer of maize’. Our previous study showed that a *helitron*-induced *ZmGDIα* variant *ZmGDIα-hel* is the recessive resistance gene, leading to quantitative resistance to MRDD. We also detected that the host ZmGA2ox7.3 can interact with either ZmGDIα or ZmGDIα-hel or viral protein P7-1. Here, we detect that ZmGA2ox7.3 binds more tightly to ZmGDIα than ZmGDIα-hel. The resulting heteromultimer P7-1/ZmGDIα/ZmGA2ox7.3 shows higher dioxygenase activity than P7-1/ZmGDIα-hel/ZmGA2ox7.3 in the conversion of biologically active gibberellins GA_1/GA_4 to inactive GA_8/GA_{34}. High-active P7-1/ZmGDIα-hel/ZmGA2ox7.3 greatly interfered with phytohormone homeostasis, thus causing the MRDD phenotype of internode shortening.

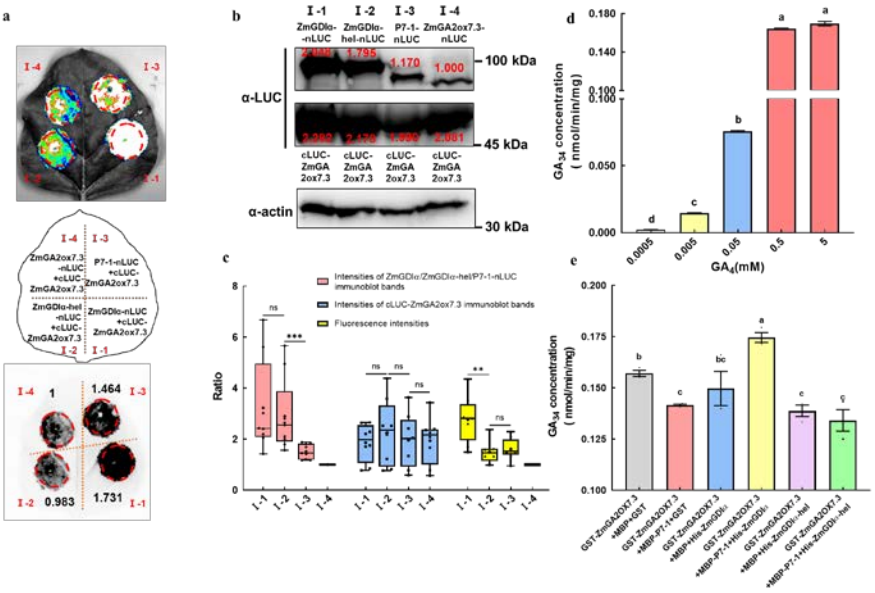


图 4、ZmGA2ox7.3/ZmGDIα/P7-1 介导玉米粗缩病病症形成。

Figure 4. ZmGA2ox7.3/ZmGDI α/ P7-1 mediates the development of symptom of MRDD.

4、玉米抗拟轮枝镰孢菌穗腐病 QTL 的精细定位

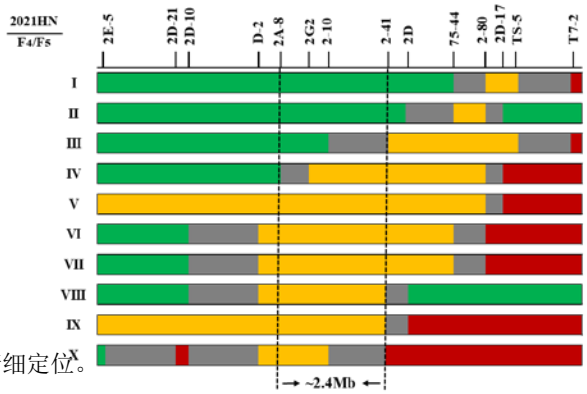
玉米穗粒腐病是世界范围内发生的危害严重的真菌性病害，不仅造成玉米产量的下降，产生的真菌毒素更对人畜的健康造成严重威胁。近年来，随着气候的变化，玉米穗粒腐病已蔓延成为玉米种植区最严重的病害，成为育种家最关心的问题。我们利用玉米穗腐病高抗材料 CML304 和感病材料 B73 组配的 RIL 群体，在玉米 2 号染色体鉴定到一个抗玉米穗腐病的主效 QTL，将其命名为 QTL-*qRfv2*，能够解释表型变异的 18.66%。2020 年冬，在海南利用 17 个重组个体的 2300 株后代对其进行精细定位，将该位点限定在分子标记 2E-5 和 2D 之间，约 7 Mb 的区间内。

在前期定位基础上，通过加密定位区间的分子标记进行了精细定位。利用 10 个新的重组类型，将 *QTL-qRfv2* 定位到分子标记 2A-8 和 2-41 之间约 2.4 Mb 的区间内，并对区间内可能的抗病基因进行了转基因载体构建。

Maize ear rot is one of the most devastating fungal diseases worldwide, which not only reduces maize yield, also the mycotoxins produced by *Fusarium* spp. can be fatal to health of human and livestock. With the climate change in latest these years, maize ear rot has spread to all maize-growing areas and become the most serious disease and the most concerned topic of maize breeders. We used the RIL population constructed by the resistant parent CML304 and the susceptible parent B73 to excavate resistance genes of *Fusarium verticillioides* ear rot in maize. A major QTL was identified on chromosome 2 of maize and named it QTL-*qRfv2*, which could explain 18.66%of phenotypic variation. We utilized 2300 maize plants, which were the offspring of the selected 17 recombinant individuals, to fine mapping the *Fusarium* ear rot resistance loci QTL-*qRfv2*. The results showed that the QTL-*qRfv2* was located on the upstream of the flanking

maker 2D, and the loci segment within about 7Mb.

In the previously identified QTL-*qRfv2* region, more molecular markers have been developed for further fine-mapping. Based on offspring derived from ten recombinants, QTL-*qRfv2* was further narrowed down to a 2.4 Mb interval flanked by markers 2A-8 and 2-41. The potential candidate genes were identified and cloned into express vector for functional validation.



Deduced Phenotype	Marker	No. of plants: Homozygote 304/304	No. of plants: Homozygote B73/B73	No. of plants: Heterozygote 304/B73	DSI(%): Homozygote 304/304	DSI(%): Homozygote B73/B73	DSI(%): Heterozygote 304/B73
S	TS-5	11	15	34	13.6^{a}	11.67^{a}	13.98^{a}
S	75-44	15	19	37	55^{a}	55.26^{a}	61.49^{a}
S	2-41	23	15	42	30.43^{a}	36.67^{a}	31.55^{a}
R	2G2	13	18	37	25^{b}	48.61^{a}	41.22^{a}
R	2-41	15	15	30	31.67^{b}	55^{a}	40.83^{b}
R	2-10	15	17	25	18.33^{b}	41.18^{a}	46^{a}
R	2G2	23	15	26	36.96^{b}	56.67^{a}	33.65^{b}
R	2-41	14	16	33	35.71^{ab}	46.88^{a}	35.61^{b}
R	2D-10	10	12	25	45^{ba}	62.5^{a}	47^{b}
R	2-10	18	14	33	13.89^{b}	28.57^{a}	27.27^{a}

图 5、*qRfv2* 精细定位。

Figure 5. Fine mapping of *qRfv2.*

5、玉米抑制光周期敏感 QTL-*qPss3* 的克隆

光周期敏感性是决定玉米能否适应高纬度地区的关键因素。抑制玉米的光周期敏感性，不仅有助于优良品种向高纬度地区的推广，也有助于降低制种的成本。尽管在玉米中发现了许多与调控开花时间相关的基因，但尚未有抑制光周期敏感性基因的报道。在我们前期研究中，发现当 *ZmCCT10* 位点具有相同的光周期敏感等位基因时，不同玉米自交系之间的光周期敏感性表现出巨大差异。由此，我们使用两套具有相同遗传背景但不同 *ZmCCT10* 等位基因的分离群体来进行数量性状基因座（QTL）分析。我们在携带 *ZmCCT10* 敏感等位基因的群体中，鉴定到了一个位于 3 号染色体上的特异主效 QTL，*qPss3*。通过连续的精细定位，我们最终将 *qPss3* 的定位区间缩小至 17kb 的物理区间。在长日照条件下，*qPss3* 以完全显性的方式通过抑制 *ZmCCT10* 诱导的光周期敏感性，促使开花期提前 2-4 天。基因注释结果显示定位的 17kb 物理区间内无预测的功能基因，而位于这段序列下游 49kb 处有一预测的功能基因 *ZmNPR1I*。我们利用 *ZmNPR1I* 的过表达材料和 CRISPR 敲除材料进行开花期鉴定，证实 *ZmNPR1I* 就是 *qPss3* 的功能基因。

Mapping of Suppressing Photoperiod Sensitivity Qtl-*Qpss3* in Maize

Photoperiod sensitivity is a key factor affecting the adaptation of maize (*Zea mays* L.) to high-latitude growing areas. Inhibiting the photoperiod sensitivity of maize is not only conducive to the promotion of some valuable varieties to high latitudes, but also helps to reduce the cost of seed production. Although many genes associated with flowering time have been identified in maize, no gene that inhibits photoperiod sensitivity has been reported. In our previous study, we detected large differences in photoperiod sensitivity among maize inbred lines with the same photoperiod-sensitive allele at the *ZmCCT10* locus. Here, we used two segregating populations

with the same genetic backgrounds but different *ZmCCT10* alleles to perform quantitative trait locus (QTL) analysis. We identified a major QTL on chromosome 3, *qPss3*, only in the population carrying the sensitive *ZmCCT10* allele. After sequential fine-mapping, we eventually delimited *qPss3* to an interval of ~17 kb. There is no annotation of functional gene in the 17kb physical interval, which is located 49kb upstream of the regulatory region of *ZmNPR1I* gene. We used overexpression and CRISPR materials of *ZmNPR1I* for flowering test and confirm that *ZmNPR1I* is the functional gene of *qPss3*.

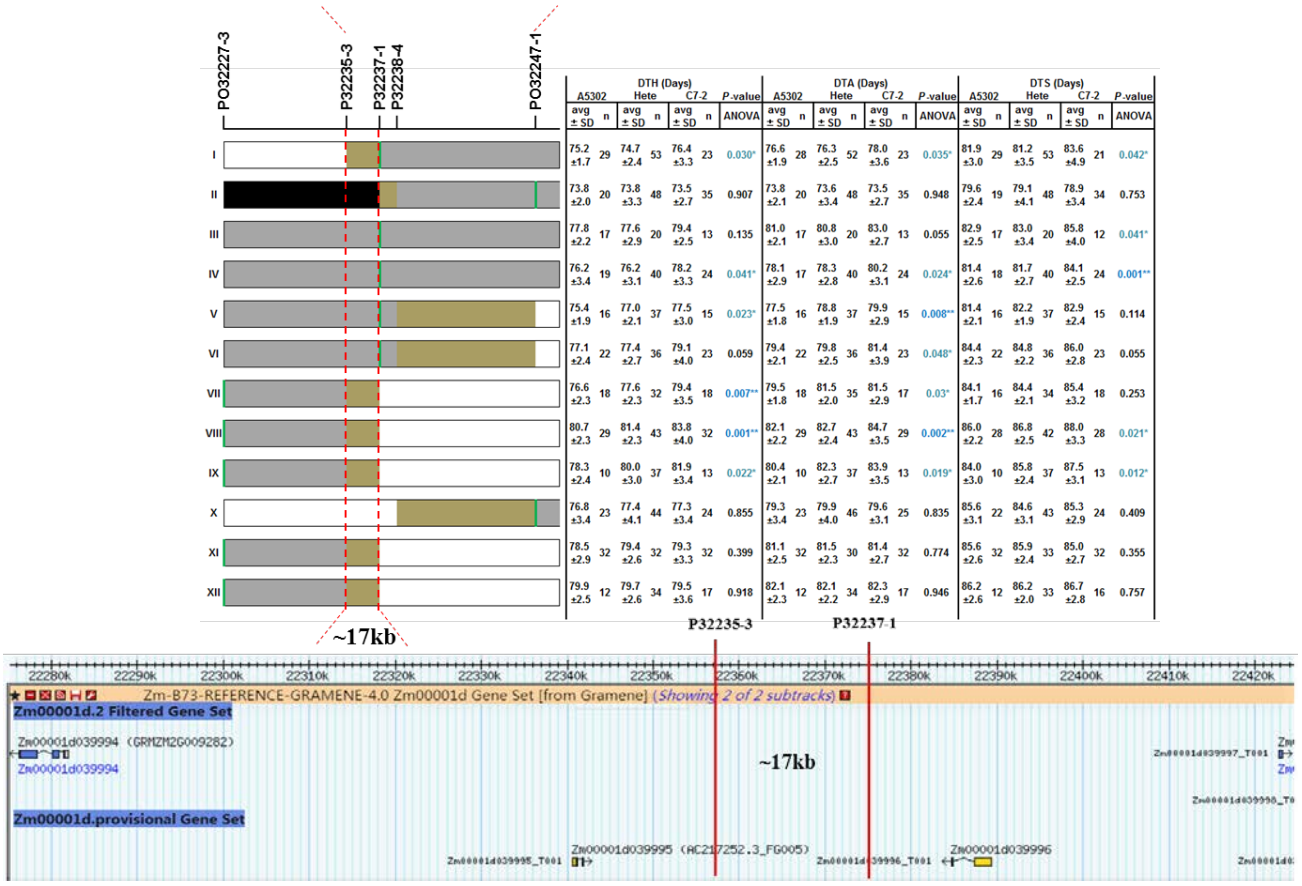


图 6、*qPss3* 的精细定位。

Figure 6. Fine mapping of *qPss3.*

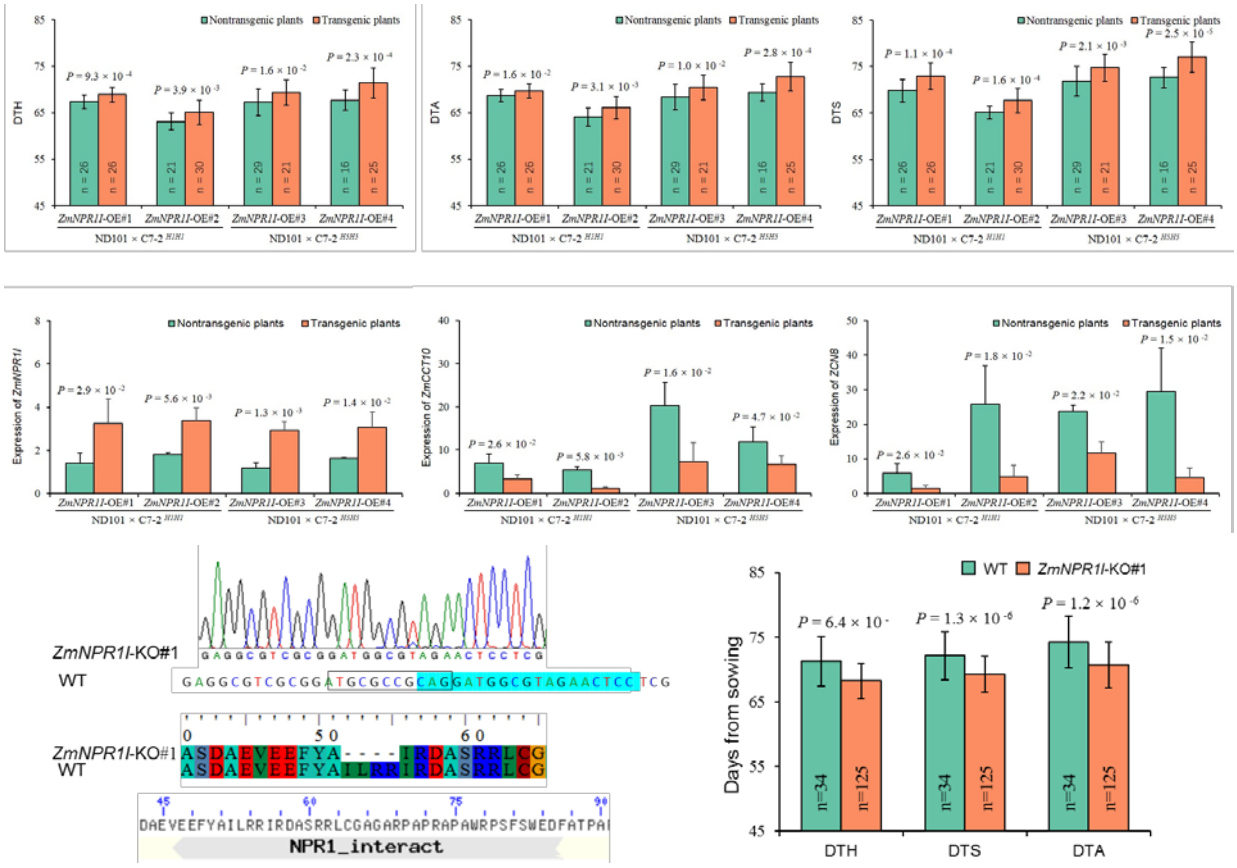


图 7、*ZmNPR1I* 转基因功能验证。

Figure 7. Transgenic validation of *ZmNPR1I*.

（二） 研究成果

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

1. Tong L, Yan M, Yang J, Li Y, **Xu M*** (2022) *ZmCCT* haplotype *H5* improves yield, stalk-rot resistance, and drought tolerance in maize. ***Front Plant Sci*** 13: 984527.
2. **Zhu M**, Ma J, Liu X, Guo Y, Qi X, Gong X, Zhu Y, Wang Y, Jiang M (2022) High-resolution mapping reveals a *Ht3*-like locus against northern corn leaf blight. ***Front Plant Sci*** 13: 968924.
3. Gou M, Balint-Kurti P, **Xu M*,** Yang Q* (2022) Quantitative disease resistance: multifaceted players in plant defense. ***J Integr Plant Biol*** https://doi.org/10.1111/jipb.13419.

专利授权

一种培育抗灰斑病植物的方法。申请人：**徐明良**，朱芒，番兴明，钟涛，**徐凌**，张艳，刘丽；专利号：ZL201910160206.3，授权日期：2022 年 05 月 10 日。

（三） 研究队伍

固定人员：

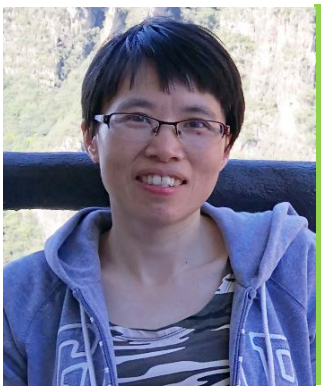
徐明良（课题组长），叶建荣。

博士后：

钟涛，朱芒，邓穗宁，张倩倩。

研究生：

徐暑晖，杜腓利，徐倩雅，刘远亮，李艳梅，郭晨煜，李蔓蔓，范周，张晓辉，闫明珠，刘玉琳，蒋思琦，陶晓波，姜晓惠，汤晟。



杨小红课题组

杨小红，教授。

研究方向：玉米高产优质性状形成的遗传基础与分子育种。

（一） 研究进展

1、玉米和水稻高产基因的发现

玉米、水稻等作物是人类能量摄入的主要来源，大约在一万年由野生种独立驯化而来。“它们在长期的驯化和改良过程中发生的相同表型变化是否遵循共同的遗传规律”一直是一个重大的基础科学问题，解决该问题对作物的遗传改良具有重要的理论和实践意义。本研究利用野生玉米资源创制了特异的穗行数为6行的玉米自交系，克隆了控制玉米穗行数的基因*KRN2*，发现了该基因上游非编码区在玉米驯化和改良过程中受到了明显的选择，导致基因表达量降低，进而增加了玉米的穗行数和穗粒数。鉴定了水稻同源基因*OsKRN2*，发现该基因与玉米*KRN2*类似，控制水稻的二次枝梗数和穗粒数，在水稻驯化和改良过程中也受到了选择。*KRN2*/*OsKRN2*编码WD40蛋白，与功能未知蛋白DUF1644互作，通过保守的分子途径负调控玉米穗行数与水稻枝梗数。在此基础之上，利用基因编辑技术分别创制了*KRN2*和*OsKRN2*基因功能丧失的新种质。在相同的遗传背景下，玉米增产10%左右，水稻增产8%左右，且未发现明显的不良效应。进一步，利用玉米、水稻及野生种的大数据进行全基因组选择分析，发现了490对玉米和水稻的趋同选择基因，并显著高于随机组合的基因对，表明趋同选择在全基因组水平上受部分约束。进一步的通路富集分析发现这些趋同选择基因在玉米和水稻特定的代谢途径中显著富集，包括淀粉和蔗糖代谢途径以及辅助因子的合成途径。本研究从单基因和全基因组水平上揭示了玉米和水稻在演化过程中发生趋同选择的遗传规律，为作物育种提供了战略基因资源，丰富了作物驯化的遗传学理论，为从头驯化或再驯化创制新型作物提供重要的理论基础（Chen et al., *Science*, 2022）。

Discovery of a Gene that Enhances Grain Yield in Maize and Rice

The major cereals, such as maize and rice, domesticated independently ~10,000 years ago and represent a primary source of human calories. During the independent process of cereal evolution, many trait shifts appear to have been under convergent selection to meet the specific needs of humans. Given the close phylogenetic relationships among cereals, a key question is whether convergent phenotypic selection in distinct lineages was driven by conserved molecular changes. Identification of convergently selected genes across cereals could help to clarify the

evolution of crop species and to accelerate breeding programs. In this study, we developed an introgression line, MT-6, with six kernel rows from the wild ancestor of maize, and identified a selected gene, *KRN2* (*kernel row number2*), that differs between domesticated maize and its wild ancestor, teosinte. This gene underlies a major quantitative trait locus for kernel row number in maize. Selection in the noncoding upstream regions resulted in a reduction of *KRN2* expression and an increased grain number through an increase in kernel rows. The rice ortholog, *OsKRN2*, also underwent selection and negatively regulates grain number via control of secondary panicle branches. These orthologs encode WD40 proteins and function synergistically with a gene of unknown function, DUF1644, which suggests that a conserved protein interaction controls grain number in maize and rice. Field tests show that knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by ~10% and ~8%, respectively, with no apparent trade-off in other agronomic traits. This suggests potential applications of *KRN2* and its orthologs for crop improvement. Furthermore, we identified a set of 490 orthologous genes that underwent convergent selection during maize and rice evolution on a genome-wide scale, including *KRN2*/*OsKRN2*. These findings show that common phenotypic shifts during maize and rice evolution acting on conserved genes are driven at least in part by convergent selection, which in maize and rice likely occurred both during and after domestication. The findings provided gene resources for crop breeding, enriched the genetic theory of crop domestication, and provided an important theoretical basis for knowledge-driven *de novo* domestication or re-domestication to create new crops (Chen et al., *Science*, 2022).

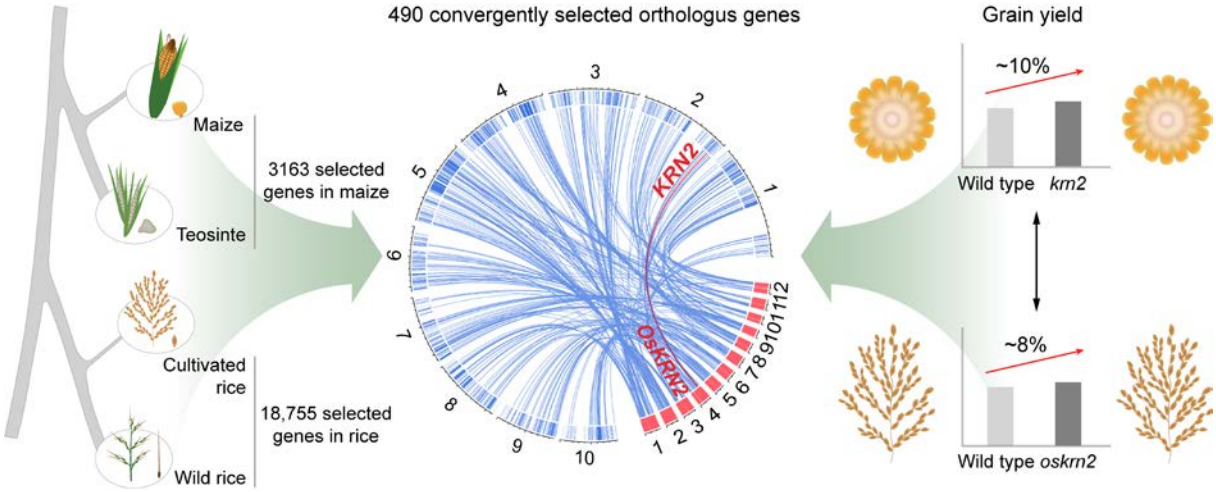


图1、玉米和水稻在演化过程中发生趋同选择的遗传规律。

Figure 1. Shared selected orthologous genes in maize and rice for convergent phenotypic shifts during domestication and improvement.

2、基于系统代谢工程的高油玉米育种新策略

玉米油是由三酰甘油（TAG）生成的脂肪酸酯混合物，是玉米食用油、饲料和生物燃料的重要

来源。商用高油玉米杂交种的籽粒含油量平均为 8%左右，远低于高油玉米品系（高达 20%）。近年来，高油玉米基因组学和遗传学的重大进展以及系统代谢工程技术的快速发展为高油玉米育种提供了新的机遇。本研究基于系统代谢工程策略提出了高油玉米培育的三个研究方向，分别为：具有高油高产特性的玉米种质创新、二十碳五烯酸（EPA）和二十二碳六烯酸（DHA）生物强化以及将玉米油生产扩大到营养生物量，这三个研究方向分别对应了将玉米作为油料作物、营养生物加工厂和能源作物三个育种目标。（1）要培育高油高产玉米种质，可以以现有的高产稳产玉米杂交种的亲本为起始材料，增加从母体植株到籽粒碳水化合物的供应，用作脂质合成的基质，参与这一代谢途径的基因包括拟南芥中将叶片中的淀粉转变为糖的 *SEX1* 和 *PGM1*，以及亚麻荠中将糖从叶片远距离运输至籽粒中的 *TST1*。此外，玉米中的 *WRI1a* 等转录因子可增加脂肪酸生物合成途径的碳通量、*ZmDGAT1-2* 可促进三酰甘油的生物合成，这些基因的过表达能够增加玉米籽粒含油量，而对产量不产生严重的影响。因此，利用这些功能和代谢途径更加明确的基因改良高油玉米，能避免对产量的不利影响。（2）二十碳五烯酸和二十二碳六烯酸是人类健康必需的天然产物，主要由海洋业生产，陆生植物因缺少极长链-3-多不饱和脂肪酸合成途径而极少产生这两种脂肪酸。玉米油中富含亚麻酸，而 α-亚麻酸的含量却极少，后者是二十碳五烯酸合成的前体物质，可由Δ^{15}-去饱和酶去饱和亚麻酸而合成。然而，亚麻酸也会被Δ^{6}-去饱和酶去饱和，因此，可利用 CRISPR–Cas9 系统和过表达去饱和/延长异构酶的方法降低Δ^{6}-去饱和酶的活性，从而使更多的亚麻酸流向 3-多不饱和脂肪酸合成途径，产生更多的二十碳五烯酸和二十二碳六烯酸。（3）对三酰甘油合成和调控、贮藏和降解等途径的认知，有助于利用代谢工程创制高含油量的营养组织，包括增加碳源的流入、提高三酰甘油的合成、提高细胞质油脂的转换效率和减缓油体的降解等四个方面，对不同代谢途径中的多个基因进行改造，更有可能产生高能量的玉米种质（Li et al., *Curr Opin Biotechnol*, 2022）。

Using Systems Metabolic Engineering Strategies for High-oil Maize Breeding

Maize oil, which is a blend of fatty acid esters generated from triacylglycerol (TAG), is an important component of maizederived food, feed, and biofuel. The kernel oil content in commercial high-oil maize hybrids averages ~8%, which is far lower than that in developed high-oil maize lines (as high as 20%). Advances in high-oil maize genomics and genetics and the development of systems metabolic engineering technologies provide new opportunities for high-oil maize breeding. In this review, we discuss the possibility of using kernels and vegetative tissues as factories to produce TAG, eicosapentaenoic acid, and docosahexaenoic acid. We further propose specific implementation strategies based on the metabolic engineering of other species to develop transgenic and gene-editing products, as well as traditional breeding strategies, for application in high-oil maize breeding programs (Li et al., *Curr Opin Biotechnol*, 2021).

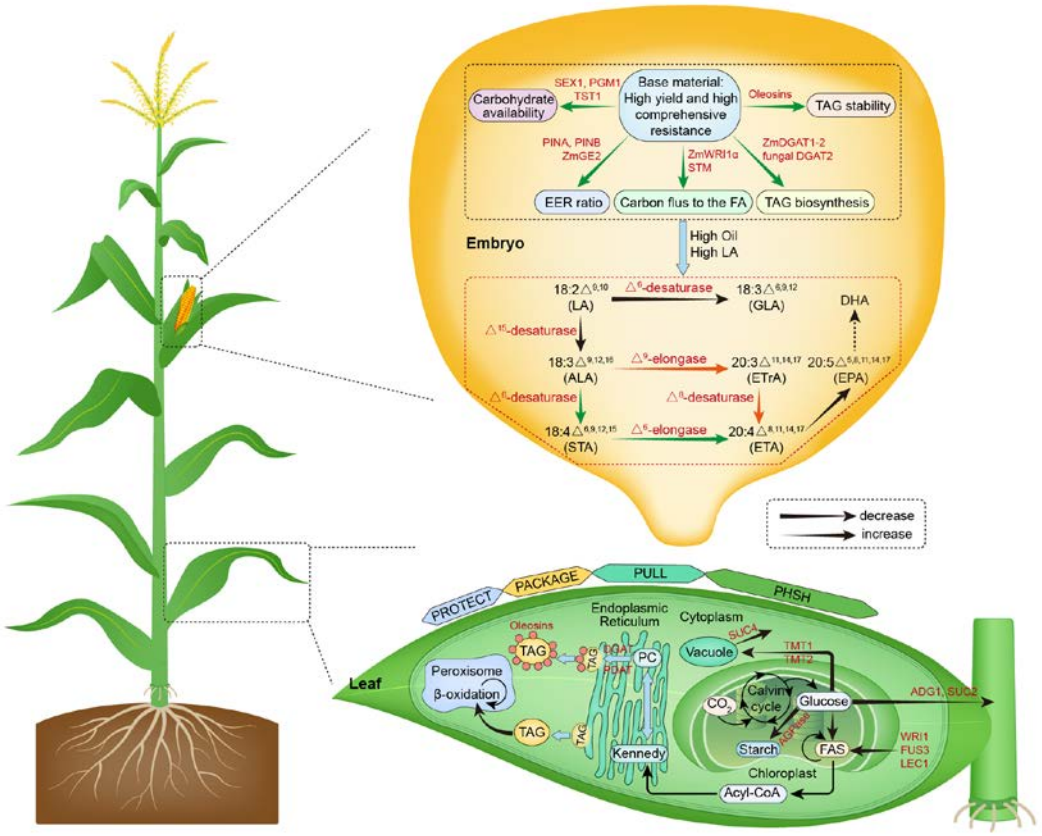


图2、三种基于代谢工程的高油玉米培育策略。

Figure 2. Three proposed metabolic engineering strategies for breeding high-oil maize.

3、利用玉蜀黍的群体基因组学解析玉米驯化和适应的遗传基础

玉米（*Zea mays* L. ssp. *mays*）大约 1 万年前在墨西哥西南部巴尔萨斯河流域由大刍草（*Zea mays* L. ssp. *parviglumis*）驯化而来，之后传播到世界各地并适应了多种环境。在过去的二十年间，研究人员致力于揭示玉米驯化和适应的过程，但在样本大小或遗传多样性方面有一定局限性。为了更好的探究玉米演化历程，我们利用 4 万多个单核苷酸多态性标记对 982 个玉米自交系和 190 个大刍草种质资源开展了全基因组范围的研究。群体结构、主成分和系统进化树等分析结果证实了大刍草到玉米的进化关系，并进一步明确了大刍草各亚种的进化谱系。单倍型分析发现玉米与 *Zea mays* ssp. *parviglumis* 和 *Zea mays* ssp. *mexicana* 之间具有相似比例的祖先等位基因，表明 *Zea mays* ssp. *parviglumis* 和 *Zea mays* ssp. *mexicana* 对玉米基因库具有重要的贡献。全基因组选择分析鉴定了 394 个驯化选择区域和 360 个适应选择区域，包含了一系列已知的驯化基因和适应基因，例如 *TB1* 和 *ZmCCT9*。模拟分析发现已发表的与花期有关的位点在这些选择区域显著富集。全基因组关联分析共鉴定到 125 个位点与花期显著关联，其中 10 个候选基因落于适应选择区域。本研究拓展了玉米驯化与适应的分子机制，为玉米的基础研究和遗传改良提供了丰富的资源（Xu et al., *BMC*

Plant Biology, 2022）。

Population Genomics of *Zea* Species Identifies Selection Signatures During Maize Domestication and Adaptation

Maize (*Zea mays* L. ssp. *mays*) was domesticated from teosinte (*Zea mays* ssp. *parviglumis*) about 9000 years ago in southwestern Mexico and adapted to a range of environments worldwide. Researchers have depicted the maize domestication and adaptation processes over the past two decades, but efforts have been limited either in sample size or genetic diversity. To better understand these processes, we conducted a genome-wide survey of 982 maize inbred lines and 190 teosinte accessions using over 40,000 single-nucleotide polymorphism markers. Population structure, principal component analysis, and phylogenetic trees all confirmed the evolutionary relationship between maize and teosinte, and determined the evolutionary lineage of all species within teosinte. Shared haplotype analysis showed similar levels of ancestral alleles from *Zea mays* ssp. *parviglumis* and *Zea mays* ssp. *mexicana* in maize. Scans for selection signatures identified 394 domestication sweeps by comparing wild and cultivated maize and 360 adaptation sweeps by comparing tropical and temperate maize. Permutation tests revealed that the public association signals for flowering time were highly enriched in the domestication and adaptation sweeps. Genome-wide association study identified 125 loci significantly associated with flowering-time traits, ten of which identified candidate genes that have undergone selection during maize adaptation. In this study, we characterized the history of maize domestication and adaptation at the population genomic level and identified hundreds of domestication and adaptation sweeps. This study extends the molecular mechanism of maize domestication and adaptation, and provides resources for basic research and genetic improvement in maize (Xu et al., *BMC Plant Biology,* 2022).

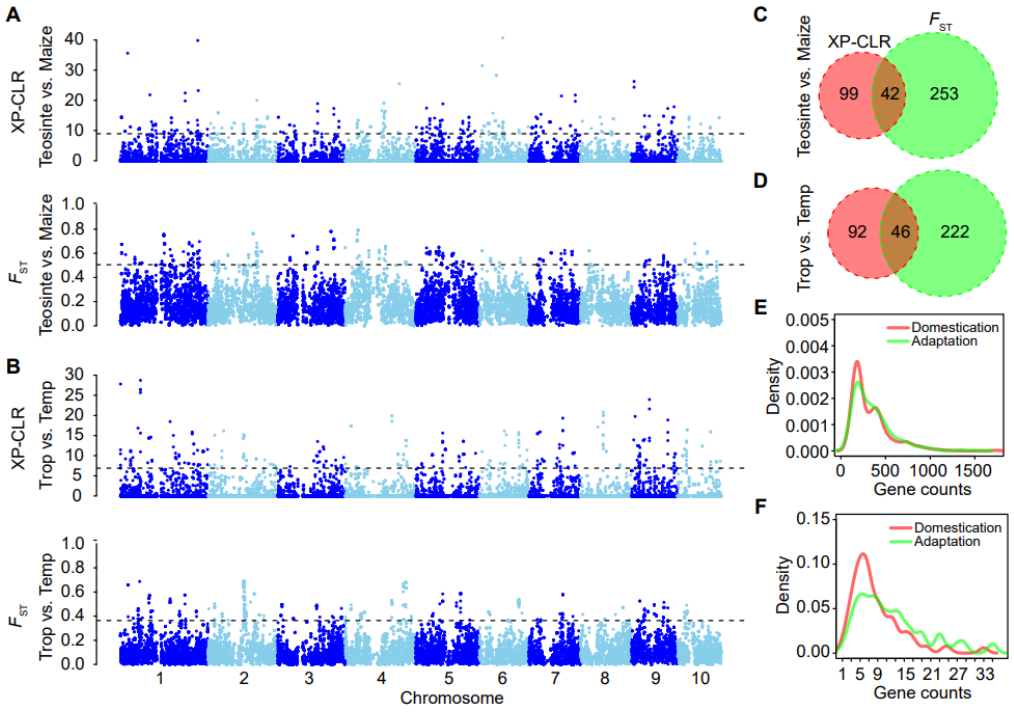


图 3、玉米驯化和适应过程中受选择位点的全基因组鉴定。

Figure 3. Genome-wide scan for regions that have undergone selection during maize domestication and adaptation.

4、玉米果穗数 QTL 及候选基因的鉴定

果穗数是玉米重要的农艺性状，单株果穗数的多少与玉米产量紧密相关。随着人们需求的多样化，多穗型玉米笋作为一种营养丰富的食材逐渐受到重视。同时，果穗数也是玉米的一个驯化性状。然而，玉米果穗数的遗传基础在很大程度上仍不清楚。我们以非多穗自交系 Mo17 和一个来自地方品种的多穗材料 LAN404 为亲本构建了 F_2 和 $F_{2:3}$ 群体，鉴定到一个影响果穗数的 QTL-*qEN7*。该 QTL 可以解释 10.7–11.9%的表型变异，来自 LAN404 的等位基因大约可以增加 1 个果穗。在此基础之上，通过精细定位将 *qEN7* 的区间缩小到 0.56 Mb，包含 8 个候选基因。选择分析、玉米不同组织的表达模式分析以及双亲间的序列多态性分析表明，一个编码 IDD 转录因子的 *Zm00001d020683* 基因最有可能是 *qEN7* 位点的候选基因。*Zm00001d020683* 在营养生长分生组织、幼穗和节间有较高的表达，并在玉米改良过程中经历了选择。*qEN7* 的鉴定及候选基因的预测为玉米果穗数的进化提供了新的线索，并为多穗型玉米品种的选育提供了新的资源（Wang et al., *Crop J*, 2022）。

Identifying QTL and Candidate Genes for Prolificacy in Maize

In maize, prolificacy, the number of ears per plant, is a trait of interest to maize breeders for

breeding high grain-yielding cultivars or specialty corn, as well as being a model trait for decoding the molecular mechanism of maize evolution. Its genetic basis remains largely unknown. We identified a stable quantitative trait locus, *qEN7*, for ear number on chromosome 7 in both F_2 and $F_{2:3}$ populations derived from a single cross between the nonprolific inbred line Mo17 and the prolific inbred line LAN404 derived from the landrace PI217404. *qEN7* explained 10.7–11.9% of phenotypic variation, and the LAN404 allele at this locus was associated with an increase of around one ear per plant. *qEN7* was confined by fine-mapping to a 0.56-Mb region containing eight annotated genes. Analysis of selection, gene expression patterns in various maize tissues, and sequence polymorphisms between the two parental lines suggested that *Zm00001d020683*, which encodes a putative INDETERMINATE DOMAIN (IDD) transcription factor, is the most likely candidate gene underlying *qEN7*. *Zm00001d020683* is expressed mainly in the vegetative meristem, immature ears, and internodes and has undergone selection during maize improvement. The identification of *qEN7* and the prediction of its candidate gene sheds some light on the evolution of maize ear number and provides a novel resource for breeding of multi-ear maize cultivars (Wang et al., *Crop J*, 2022).

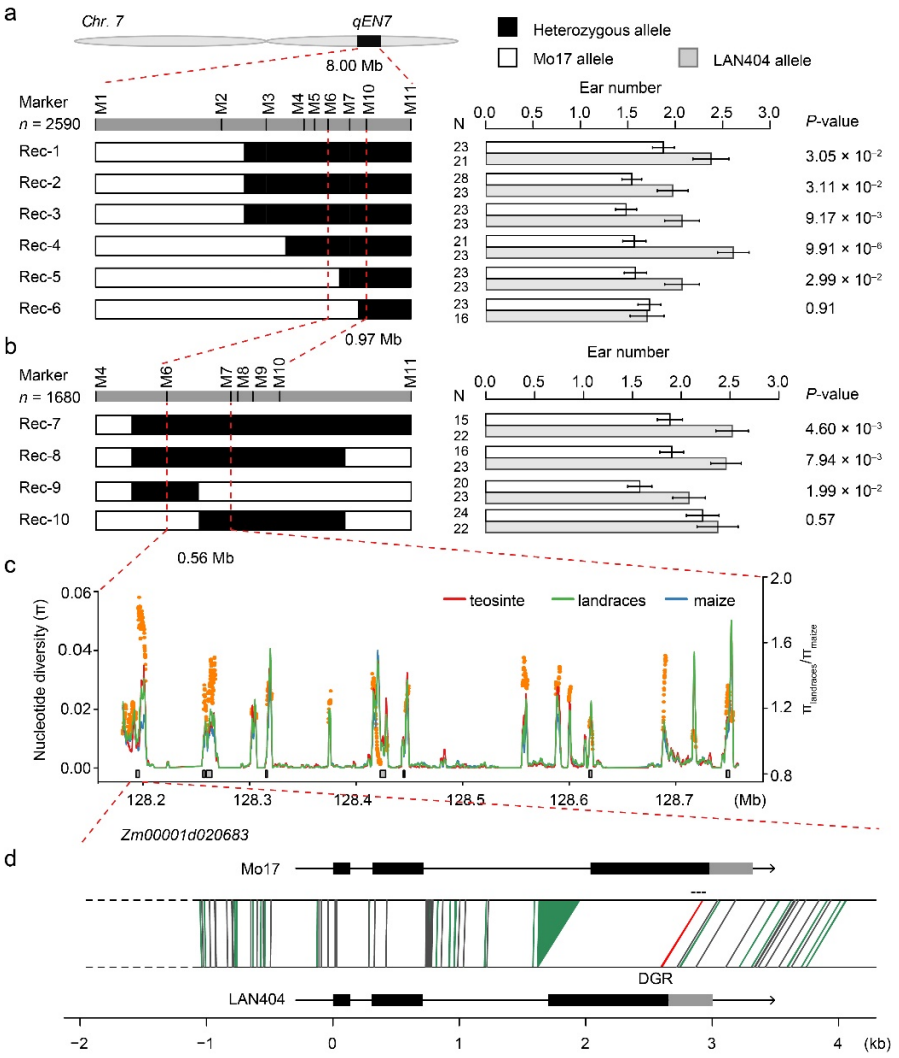


图 4、*qEN7* 的精细定位及候选基因预测。

Figure 4. Map-based cloning of *qEN7* and prediction of candidate genes.

（二） 研究成果

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

1. Chen W#, Chen L#, Zhang X#, Yang N#, Guo J, Wang M, Ji Sheng, Zhao X, Yin P, Cai L, Xu J, Zhang L, Han Y, Xiao Y, Xu G, Wang Y, Wang S, Wu S, Yang F, Jackson D, **Cheng J**, Chen S, Sun C, **Qin F**, **Tian F**, Fernie A, Li J*, Yan J*, **Yang X*** (2022) Convergent selection of a WD40 protein that enhances grain yield in maize and rice. ***Science*** 375: eabg7985.
2. Li H*, Fernie A, **Yang X*** (2022) Using systems metabolic engineering strategies for high-oil maize breeding. ***Curr Opin Biotechno*** 79:102847.
3. Xu G#, Zhang X#, Chen W#, Zhang R#, Li Z, Wen W, Warburton M, Li J, Li H*, **Yang X*** (2022) Population genomics of *Zea* species identifies selection signatures during maize domestication and adaptation. ***BMC Plant Biology*** 22: 72.
4. Wang M#, Zhang R#, Zhao Y, Yao J, Li W, Yang Z, Sun F, **Yang X*** (2022) Identifying QTL and candidate genes for prolificacy in maize. ***Crop J***. In Press

（三） 研究队伍

固定人员：

杨小红（课题组长）。

博士后：

张人予，陈文康，张璇。

研究生：

赵炳浩，孙飞，员涛，郭江华，冯海鹰，杜晓夏，赵翔宇，季生辉，殷鹏飞，王正琪，杨艳艳，李亚茹，陈真远，梁家琛，于智宏，朱林，徐丝璇。

宋任涛课题组

宋任涛，教授。

研究方向：（1）玉米籽粒发育的调控网络研究；（2）玉米蛋白品质的分子遗传学研究。

（一） 研究进展

玉米籽粒永久型胚乳形成的分子机制

单子叶植物种子和双子叶植物种子在胚乳发育方面存在显著的不同：以玉米为代表的单子叶植物的胚乳在发育过程中不断合成和积累营养物质，成熟时胚乳占据整个种子的绝大部分，因而形成永久型的胚乳；而以拟南芥为代表的双子叶植物的胚乳在发育过程中不断被胚消耗，种子成熟时仅残存最外一层胚乳，这种胚乳称之为瞬时型胚乳。虽然这两种胚乳的发育模式早被熟知，但控制这两种胚乳形成的分子机制仍不清楚。该研究鉴定到一个新的玉米籽粒突变体 *endosperm breakdown1*（*enb1*），其胚乳在籽粒发育过程中发生剧烈的降解，而胚发育正常。*enb1* 突变体的这种发育模式类似于双子叶植物种子的发育。通过对 *enb1* 突变体的基因克隆，发现 *ENB1* 编码一个在玉米籽粒基底胚乳传递层细胞中优势表达的纤维素合成酶 5。*enb1* 突变导致传递层细胞的壁内突急剧减少，进而显著降低了传递层细胞吸收蔗糖的功能。*enb1* 突变体中受损的传递层细胞功能触发了胚乳降解，胚乳淀粉降解产生的糖被转运至胚中，供给胚发育。此外，*ENB1* 过表达增强传递层细胞壁内突的发育，促进蔗糖通过传递层细胞转运至胚乳中，进而增加籽粒的粒重。此项研究证实了 ENB1 是合成基底胚乳传递层细胞壁内突的关键因子，并揭示了玉米籽粒永久型胚乳形成的分子机制（Wang et al., *Plant Cell*, 2022）。

Molecular Mechanism of Persistent Endosperm Formation in Maize Kernel

Development of the endosperm is strikingly different in monocots and dicots. Generally, in monocots such as maize (*Zea mays*), the endosperm is a persistent tissue that synthesizes and accumulates large amounts of nutrient reserves during seed development, and ultimately occupies the largest portion of the mature seed. Whereas in dicots, such as *Arabidopsis* (*Arabidopsis thaliana*), the endosperm is a transient tissue and is largely consumed during embryo development, leaving one layer of cells at maturation. Although these developmental patterns are well-known, little is known about the controlling mechanisms responsible for these different endosperm fates. This study characterized a novel maize kernel mutant, *endosperm breakdown1* (*enb1*), in which the typically persistent endosperm was drastically degraded during kernel development, while its embryo was normally developed. This developmental pattern of *enb1*

endosperm was similar to that of dicots. Map-based cloning of *enb1* mutant revealed that *ENB1* encodes a cellulose synthase 5 that is predominantly expressed in the basal endosperm transfer layer (BETL) of endosperm cells. *enb1* mutation caused a drastic reduction in the formation of cell wall ingrowths (CWIs) in BETL cells, impairing the sucrose uptake function of BETL cells. In *enb1*, the defective function of BETL cells resulted in premature utilization of endosperm starch to nourish the embryo. Overexpression of *ENB1* enhanced the development of CWIs, facilitating sucrose transport into endosperm via BETL cells and increasing kernel weight. This study demonstrated that ENB1 is a key factor for synthesizing CWIs in BETL cells and revealed a mechanism for the formation of persistent endosperm in the maize kernels (Wang et al., *Plant Cell*, 2022).

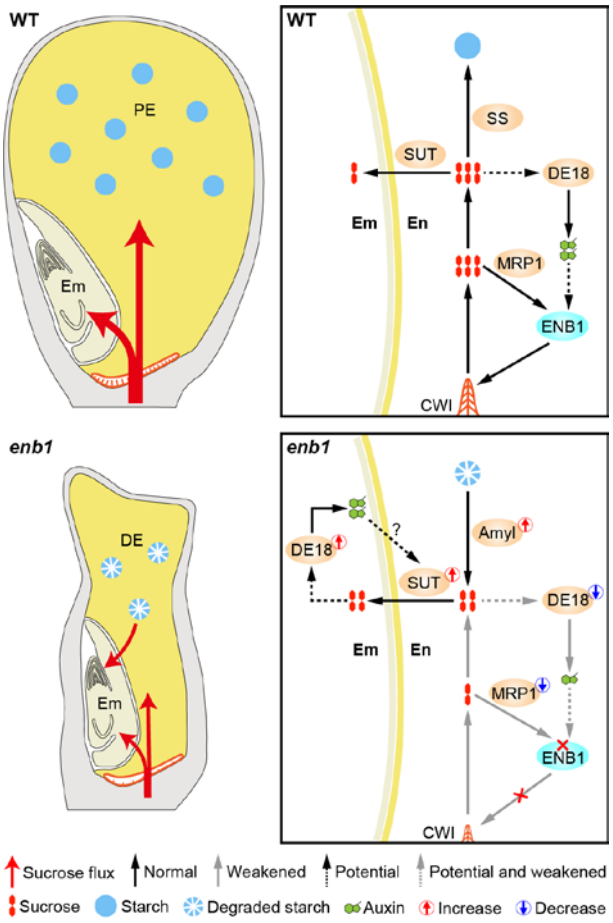


图 1、ENB1 合成的传递层细胞壁内突维持了永久型胚乳发育的模型。

Figure 1. Model illustrating that CWIs synthesized by ENB1 sustain development of a persistent endosperm.

（二） 研究成果

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

Wang Q, Wang M, Chen J, Qi W, Lai J, Ma Z, **Song R*** (2022) *ENB1* encodes a cellulose synthase 5 that directs synthesis of cell wall ingrowths in maize basal endosperm transfer cells. ***Plant Cell*** 34: 1054-1074.

（三） 研究队伍

固定人员：

宋任涛（课题组长）。

博士后：马泽阳，王群。

研究生：

袁跃，陈艳花，宋滕，梁磊，张子如，张伟潇，霍强，陈义聪，刘迎，刘紫林，黎孟菲，巩崇智，孙茜，张克春，黄龙，韩艳斌，叶欣雨，贾苏豪，闫佳慧，张帅。

田　丰

课题组

田丰，教授。

研究方向：玉米驯化与适应的分子遗传机制。

（一） 研究进展

1、开花期 QTL *DTP3-3* 的克隆

开花期是重要的适应性性状，玉米花期适应性的不断提高为玉米克服光周期敏感、适应更广泛的生态地理环境发挥了重要作用。课题组前期利用玉米-大刍草 BC_2S_3 渗入系群体对开花期进行了 QTL 定位分析，在玉米第 3 染色体上检测到一个效应相对较大的 QTL，命名为 *qDTP3-3*，来自大刍草的等位基因延迟开花。进一步构建 *qDTP3-3* 的近等基因系，结果表明，在长日照条件（北京）下，NIL（W22）比 NIL（8759）显著早开花 2.5 天左右，而在短日照条件（海南）下，NIL（W22）和 NIL（8759）之间的花期表型差异并不显著（图 2A）。该结果说明 *qDTP3-3* 受光周期的调控。通过对 *qDTP3-3* 进行精细定位，采用重组交换单株衍生后代表型测验的策略，对纯合重组体和纯合非重组体的表型进行测定和比较，综合重组交换单株家系多年的表型效应，最终将 *qDTP3-3* 定位在 373bp 区间（图 2B），该定位区间位于候选基因的启动子。为了进一步研究 *qDTP3-3* 候选基因是否具有调控玉米开花的生物学功能，本研究构建了候选基因的 CRISPR/Cas9 敲除系，结果显示两个敲除系事件基因移码突变，翻译提前终止，两个事件均比野生型材料显著晚开花 2-3 天（图 2C），从而证实候选基因生物学功能。

Positional Cloning of Maize Flowering Time QTL- *DTP3-3*

As an important adaptive trait, the changes in flowering time can significantly help maize overcome photoperiod sensitivity and adapt to a wider range of ecological and geographical environments. We detected a maize flowering time QTL *qDTP3-3* on chromosome 3 previously and the teosinte allele at *qDTA3-3* flowered later than the lines homozygous for the maize allele. To further evaluate the phenotypic effects of *qDTA3-3*, we planted the two NILs for *qDTA3-3* and compared their phenotypic differences. NIL (W22) flowered 2.5 days earlier than NIL (8759) under natural long days (Beijing), while the difference between NIL (W22) and NIL (8759) under short day conditions (Hainan) was not significant (Figure 2A). These results indicated that *qDTA3-3* was sensitive to differences in day length. We performed fine mapping by comparing the phenotypic difference between homozygous recombinants (HRs) and homozygous

nonrecombinants (HNRs) within each recombinant-derived F_3 family. By integrating the phenotypic effects of recombinants over many years, *qDTA3-3* was delimited to a 373 bp physical region upstream an annotated gene (Figure 2B). To validate the function of the candidate gene, CRISPR/ Cas9 technology was used to generate homozygous mutants. Two null mutants flowered 2-3 days later than wild-type plants (Figure 2C), thus verifying the biological function of the candidate gene for *qDTA3-3*.

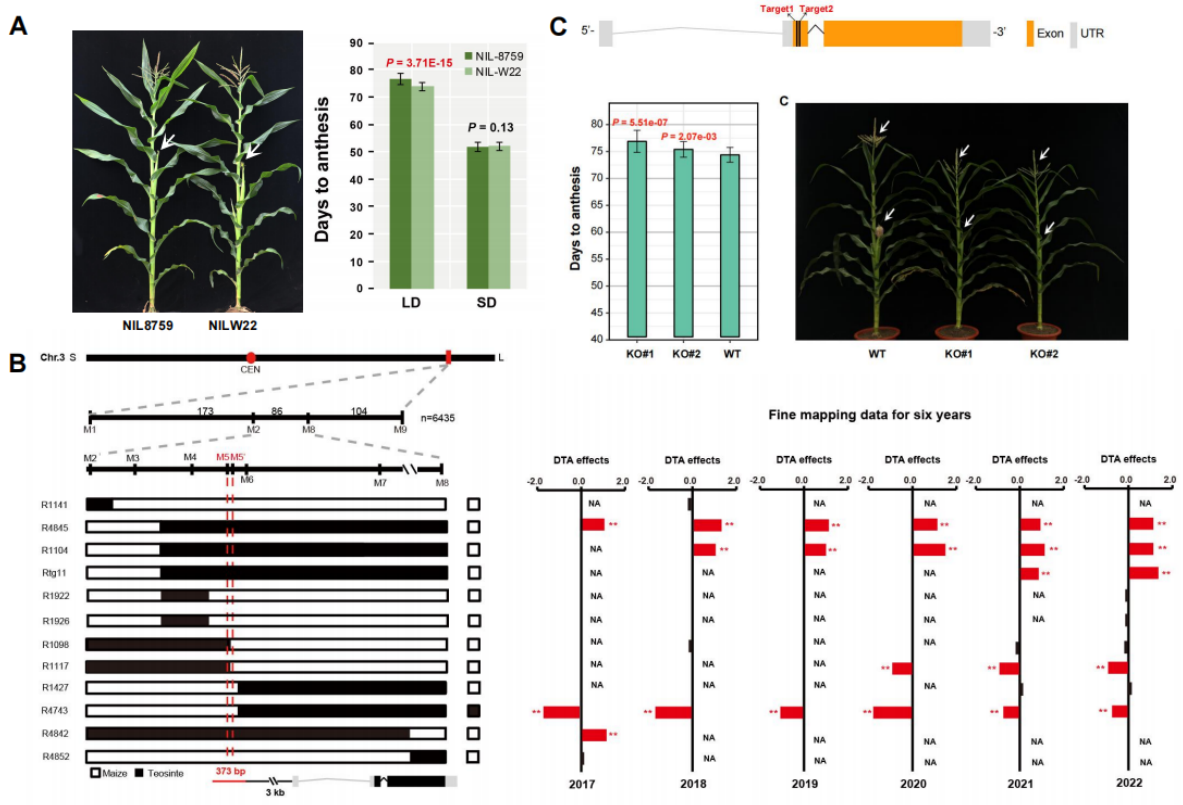


图1、玉米开花期QTL *qDTP3-3*精细定位和候选基因功能验证。

Figure 1. Fine mapping and functional verification of maize flowering time QTL *qDTP3-3.*

2、耐密株型 *DPA1* 的克隆与功能解析

密植是实现玉米产量持续增加的重要栽培措施，提高玉米种植密度是我国进一步提高玉米单产水平的重要途经。理想耐密株型通常要求上部叶片上冲，而中下部叶片相对平展。在密植条件下，这种株型能够使群体上部透光率高，群体中下部叶片处于较好的光照状态下，因此可以提高群体的光合作用效率，获得更高的群体产量。实验室前期鉴定到一个具有上部叶位夹角较小、中下部叶位夹角相对舒展的耐密理想株型特征材料，通过表型分析发现该株型受隐性单基因控制，进一步通过图位克隆发现该株型受dpa1（*density-tolerant plant architecture 1*）调控，其功能变异为第一外显子上一个273bp的转座子插入（图1）。为了验证dpa1的生物学功能，对dpa1进行了转基因功能验证，研究发现dpa1过表达植株叶夹角显著增大，株型更为松散，而dpa1敲除植株叶夹角减少，株型更为

紧凑，说明dpa1是一个叶夹角正向调控因子。对叶夹角相关基因的表达模式分析分析发现，dpa1在实验室先前克隆的叶夹角基因*ZmRAVL1*的敲除系中显著下调。进一步的EMSA、ChiP-qPCR等实验证实ZmRAVL1可直接结合dpa1启动子，激活dpa1的表达。为了评估dpa1在杂交种中的利用价值，利用dpa1和其敲除系构建了F_1杂交种，进行了不同种植密度的小区产量实验，结果表明：dpa1在杂交种背景下具有显著的密植增产效应（图1）。

Cloning and Functional Analysis of *Density-Tolerant Plant Architecture 1*

Dense planting is a vital cultivation practice to achieve a continuous increase in maize yields. Increasing planting density is a major strategy to enhance maize yields in China. An ideotype for dense planting requires upright leaf angles in the upper canopy, less erect leaves in the middle canopy and relatively flat leaves in the lower canopy. It reduces mutual shading and increases solar irradiation penetration, thus improving population photosynthesis efficiency and ultimately higher grain yield under dense planting. We identified a natural mutant possessing ideotype feature and found that it was controlled by a single recessive gene. Further fine mapping identified the mutant was regulated by dpa1 (*density-tolerant plant architecture 1*) containing a 273-bp transposon insertion in the first exon. To validate the function of dpa1, we overexpressed dpa1 and knocked out dpa1 using CRISPR-Cas9. We found that overexpression of dpa1 led to larger leaf angle, while dpa1 knockout lines exhibited smaller leaf angle, indicating that dpa1 functions as a positive regulator of maize leaf angle. We found dpa1 was significantly downregulated in the knockout plants of *ZmRAVL1*, a crucial regulator in controlling leaf angle we previously cloned. Further Y1H, EMSA and ChIP-qPCR showed that ZmRAVL1 could directly bind dpa1 promoter in vitro and in vivo to activate dpa1 expression. To evaluate the potential value of dpa1, we constructed improved and original F_1 hybrids under three different planting densities in two locations in 2022. The results showed the improved F_1 hybrid showed higher grain yield than the original F_1 hybrid in high density planting.

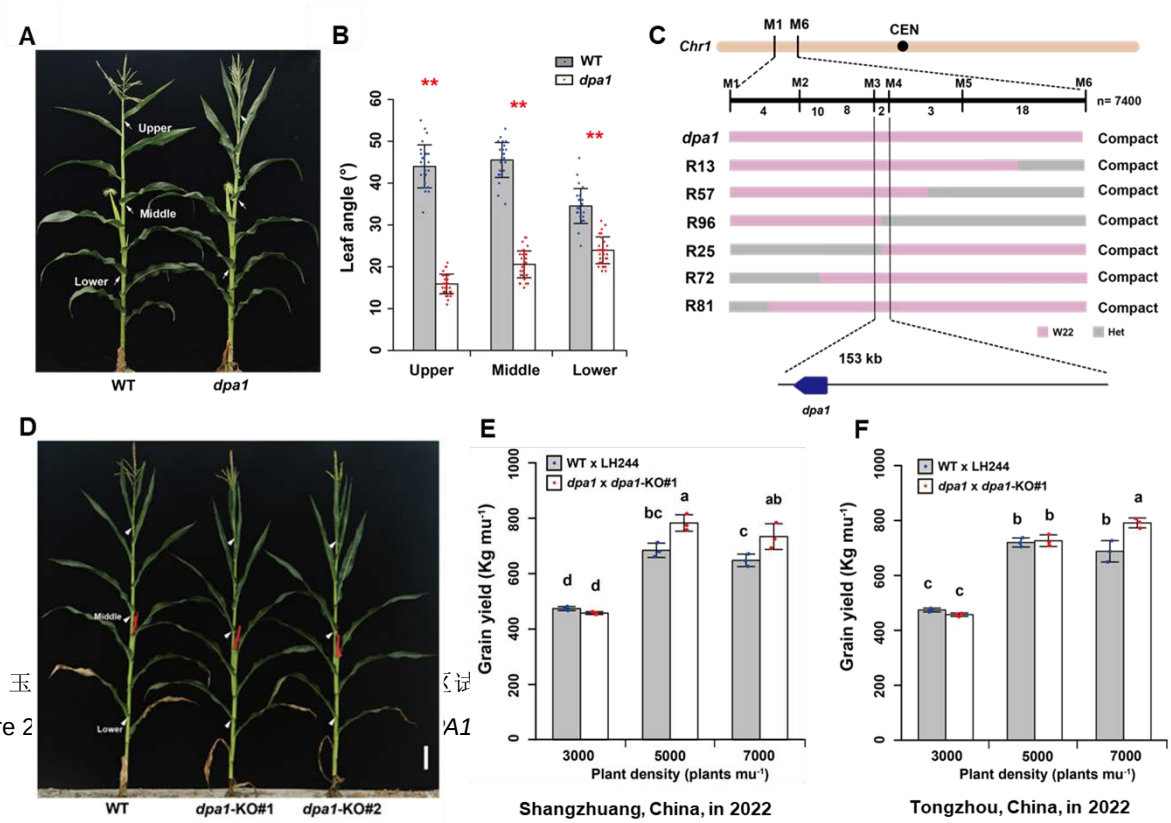


图2、玉

Figure 2

（二） 研究成果

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

Liang Y and **Tian F*** (2022) Plant genetics: mechanisms of wild soybean adaptation. ***Curr Biol***, In Press

（三） 研究队伍

固定人员：

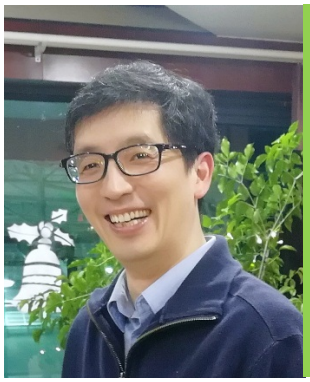
田丰（课题组长）。

博士后：

王成龙，郭丽，梁亚盟，任如昌。

研究生：

王雪涵，吴维皓，夏进良，韩旭，赵思航，秦文超，贾宏，王淑敏，陈丰懿，祝一帆，何俊杰，杜贤，杨宏，陈天贺，王一博，唐俊祥，李浩。



郑绍建课题组

郑绍建，教授。

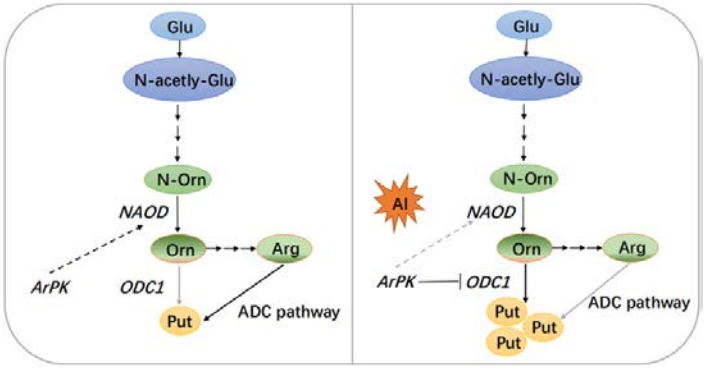
研究方向：植物响应营养逆境的分子生理机制。

（一） 研究进展

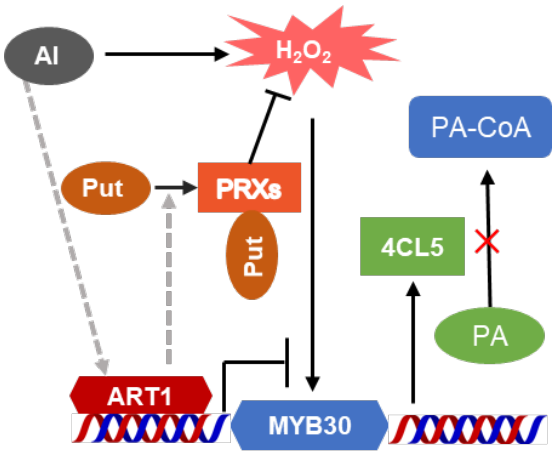
1、解析腐胺在调控水稻抗铝性中的功能及作用机制

铝是地壳中丰度最高的金属元素，主要以铝硅酸盐矿物形式存在。在酸性条件下，部分矿物态铝会被解离，并以离子态进入土壤溶液中。微摩尔级的Al^{3+}可以在短时间内抑制植物根系的生长，影响其对水分和养分吸收的功能，导致作物减产。因此，铝毒害是限制酸性土壤中植物生长尤其是农作物生产的主要环境因子。水稻作为抗铝性较高的禾本科作物，拥有较为复杂的抗铝机制。虽然迄今已明确了以转录因子ART1在调控水稻抗铝中发挥重要功能，但是否存在独立于ART1的其他抗铝机制仍有待进一步探明。

我们首先从水稻 EMS 库筛选获得的一个专一对铝敏感的突变体，通过 MutMap 定位到一个未知功能的激酶基因产生了突变表型，故将此基因命名为 *ArPK*（*Aluminum related Protein Kinase*）。GUS 染色及 qRT-PCR 结果显示，*ArPK* 在根中受铝诱导强烈表达；原位免疫荧光定位及烟草瞬转结果表明 *ArPK* 具有质膜及细胞核中双定位模式。通过转录组分析发现 *arpk* 中精氨酸代谢途径中的乙酰鸟氨酸脱乙酰基酶 *NAOD* 被组成型抑制，而鸟氨酸脱羧酶 *ODC1* 受铝诱导强烈上调达 10 倍以上，检测腐胺 Put 含量发现铝处理下突变体中自由态、结合态及束缚态腐胺含量均显著增加，暗示 Put 合成过程的紊乱可能影响了 *arpk* 的抗铝性。进一步实验发现 *CaMV35S* 启动的 *NAOD* 转入 *arpk* 中后，不能恢复突变体的铝敏感表型，而 ODC 的特异性抑制剂 DFMO 处理可以恢复 *arpk* 的铝敏感表型，表明 *ODC1* 上调是 *arpk* 中三种形态的 Put 积累进而引起水稻抗铝性降低的根本原因，ArPK 是 *ODC1* 的内源抑制子，调控铝处理下 Put 的生物合成及稳态，而 *NAOD* 组成型抑制的原因还有待进一步研究。上述研究揭示一个新蛋白激酶 ArPK 通过促进 ODC 依赖的 Put 合成影响水稻抗铝性的新机制（Liu et al; *Plant Cell Enviro*n, 2022）。



既然 Put 代谢和累积影响水稻抗铝性，进一步研究发现外源 Put 可部分恢复铝毒造成的 *art1* 根长被显著抑制的表型，并减少 *art1* 根尖特别是细胞壁中的铝积累量；同时，Put 从自由态向束缚态转化的比例也恢复至与野生型类似的水平。添加自由态向束缚态转化的抑制剂菲咯啉（o-phen）则加剧了铝毒对野生型主根伸长的抑制。暗示 ART1 可能通过影响自由态 Put 向束缚态转化的比例来改变细胞壁对铝的结合能力进而调控水稻抗铝性。铝胁迫条件下 *art1* 中调节苯丙烷代谢的候选转录因子 *OsMYB30* 显著上调，而 Put 降低其表达；而 *OsMYB30* 敲除突变体（*osmyb30-1* 和 *osmyb30-2*）的抗铝性明显高于野生型。酵母单杂交等实验表明 ART1 可直接结合于 *OsMYB30* 启动子上并抑制 *OsMYB30* 的表达；*art1-osmyb30* 双突变体则部分恢复了 *art1* 突变体的铝敏感表型。这些结果表明 ART1 直接结合 *OsMYB30* 启动子并抑制其表达。进一步研究发现 OsMYB30 直接结合编码 4-香豆酸辅酶 A 连接酶的 *Os4CL5* 启动子并激活其表达，*OsMYB30* 及 *Os4CL5* 敲除突变体抗铝性均高于野生型且细胞壁结合的该酶的底物之一对香豆酸（4-coumaric acid, PA）含量更高，铝积累量更低。推测 OsMYB30 通过正调控 *Os4CL5* 改变细胞壁结合铝的能力。此外，Put 可以降低铝诱导的根尖 H_2O_2 的水平来降低 *OsMYB30* 的表达，进而提高水稻的抗铝性。上述研究一方面阐明了 Put 调控水稻抗铝性的内在分子机制，另一方面揭示了一个新的参与铝胁迫下通过调控细胞壁修饰而影响水稻抗铝性的新转录因子（Gao et al., *J Integr Plant Biol,* 2022）。



A Novel Kinase Subverts Aluminum Resistance by Boosting Ornithine Decarboxylase-Dependent Putrescine Biosynthesis

Rice, as one of the most aluminum (Al) resistant cereal crops has developed more complicated Al resistance mechanisms than others. By using forward genetic screening from a rice EMS mutant library, we obtained a mutant showing specifically high sensitivity to Al. Through MutMap analysis followed by a complementation test, we identified the causal gene, *Al related Protein Kinase* (*ArPK*) for Al-sensitivity. *ArPK* expression was induced by a relatively longer exposure to high Al concentration in the roots. The result of RNA-seq indicated the functional disorder in arginine metabolism pathway with down-regulation of *N-acetylornithine deacetylase* (*NAOD*) expression and up-regulation of *Ornithine decarboxylase1* (*ODC1*) expression in *arpk* mutant. Al specifically and rapidly up-regulated *ODC1* expression and caused over accumulation of putrescine (Put), while the ODC inhibitor DFMO (difluoromethylornithine) reverted Al-sensitive phenotype of *arpk*, suggesting that over accumulation of endogenous Put might be harmful for root growth, and that ArPK seemed to act as an endogenous inhibitor of *ODC1* action to maintain

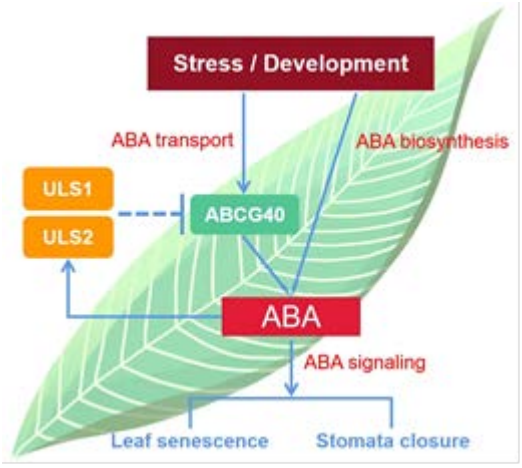
suitable endogenous Put level under Al treatment. Overall, we identified *ArPK* and its putative repressive role in controlling a novel ODC-dependent Put biosynthesis pathway specifically affecting rice Al resistance, thus enriching the fundamental understanding of plant Al resistance.

ART1 and Putrescine Contribute to Rice Aluminum Resistance Via Osmyb30 in Cell Wall Modification

Cell wall is the first physical barrier to aluminum (Al) toxicity. Modification of cell wall properties to change its binding capacity to Al is one of the major strategies for plant Al resistance, nevertheless, how it is regulated in rice remains largely unknown. In this study, we showed that exogenous application of putrescines (Put) could significantly restore the Al resistance of *art1*, a rice mutant lacking the central regulator Al RESISTANCE TRANSCRIPTION FACTOR 1 (ART1), and reduce its Al accumulation particularly in the cell wall of root tips. Based on RNA-sequencing, yeast-one-hybrid and EMSA assays, we identified an R2R3 MYB transcription factor OsMYB30 as the novel target in both ART1-dependent and Put-promoted Al resistance. Furthermore, transient dual-luciferase assay showed that ART1 directly inhibited the expression of *OsMYB30*, and in turn repressed Os*4CL5*-dependent 4-coumaric acid (PA) accumulation, hence reducing the Al-binding capacity of cell wall and enhancing Al resistance. Additionally, Put repressed *OsMYB30* expression by eliminating Al-induced H_2O_2 accumulation, while exogenous H_2O_2 promoted *OsMYB30* expression. We concluded that ART1 confers Put-promoted Al resistance via repression of OsMYB30-regulated modification of cell wall properties in rice.

2、ABA 调控叶片衰老和气孔关闭的新机制

叶片衰老是植物生长发育的一个重要过程。在叶片衰老时，细胞内叶绿体的碳同化作用转变成叶绿素和大分子物质的分解代谢，使得叶子生长阶段积累的细胞物质转化为可输出的营养物质，供给需要的器官组织。叶片衰老受到诸多信号影响，包括营养和激素信号、水分状况、光照状况和温度变化等。其中植物激素脱落酸（ABA）是促进叶片衰老最关键的信号之一，不仅外源施加 ABA 能够诱导衰老相关基因的表达，促进叶绿素降解，导致叶片衰老；而且多种生物和非生物胁迫都能提高叶片内源 ABA 水平，使得叶片衰老加速。尽管以往研究发现 ABA 生物合成和信号转导是调控叶片衰老的重要因素，但 ABA 转运是否在叶片衰老过程中发挥作用以及 ABA 转运本身如何受到调控尚不清楚。



我们发现在拟南芥中发现两个在衰老叶片高表达且高度同源的 RING-box 基因 *UBIQUITIN LIGASE of SENESCENCE 1/2*（*ULS1/2*），其双突变体 *uls1/uls2* 表现出显著的叶片提前衰老表型，

并且该表型特异性受到 ABA 促进。研究发现，在相同生长阶段的叶片中，*uls1/uls2* 比野生型积累更多的 ABA，同时 *ULS1* 和 *ULS2* 本身的基因表达受 ABA 诱导。通过转录组与泛素化蛋白质组分析发现，ABA 转运蛋白 ABCG40 在 *uls1/uls2* 中具有显著较高的表达和蛋白累积，这可能是导致叶片提前衰老的原因。进一步通过遗传学分析发现，*ABCG40* 功能 缺失突变可以明显抑制 *uls1/uls2* 叶片中的 ABA 含量，进而抑制叶片提前衰老和气孔关闭表型。该研究在遗传学上首次证明了 ABCG40 依赖的 ABA 转运过程在叶片衰老调控中的重要作用。同时，在植物生长发育过程中，叶片衰老需要受到精确调控，提前或延迟衰老都对植物不利，该研究发现 ABA 信号存在一种新的负反馈调节机制，即通过 ULS1/2-ABCG40 模块反馈抑制 ABA 转运，从而防止 ABA 信号对叶片衰老和气孔关闭过程产生过度调控，拓展了人们对 ABA 信号转导机制的认识（Wei et al., *J Integr Plant Biol*, 2022）。

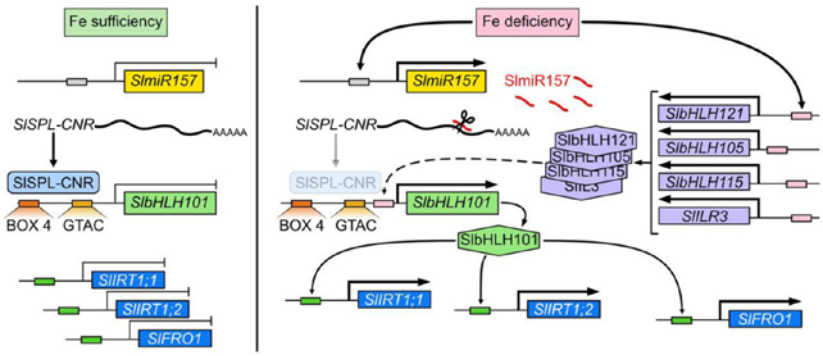
RING-Box Proteins Regulate Leaf Senescence and Stomatal Closure Via Repression of ABA Transporter Gene *ABCG40*

Plant hormone ABA plays an indispensable role in the control of leaf senescence, during which ABA signaling depends on its biosynthesis. Nevertheless, the role of ABA transport in leaf senescence remains unknown. Here, we identified two novel RING-box protein-encoding genes *UBIQUITIN LIGASE of SENESCENCE 1* and *2* (*ULS1* and *ULS2*) involved in leaf senescence. Lack of *ULS1* and *ULS2* accelerates leaf senescence, which is specifically promoted by ABA treatment. Furthermore, the expression of senescence-related genes is significantly affected in mature leaves of *uls1/uls2* double mutant (versus wild type) in an ABA-dependent manner, and the ABA content is substantially increased. *ULS1* and *ULS2* are mainly expressed in the guard cells and aging leaves, and the expression is induced by ABA. Further RNA-seq and quantitative proteomics of ubiquitination reveal that ABA transporter ABCG40 is highly expressed in *uls1/uls2* mutant versus WT, though it is not the direct target of ULS1/2. Finally, we show that the acceleration of leaf senescence, the increase of leaf ABA content, and the promotion of stomatal closure in *uls1/usl2* mutant are suppressed by *abcg40* loss-of-function mutation. These results indicate that ULS1 and ULS2 function in feedback inhibition of ABCG40-dependent ABA transport during ABA-induced leaf senescence and stomatal closure.

3、miR157-SPL-CNR 模块作用于 bHLH101 的上游负调控番茄的缺铁反应

铁（Fe）稳态对于植物的生长、发育和胁迫响应至关重要，受到复杂的调控网络的严格控制，其中转录因子（TFs）起着核心作用。已有一系列 bHLH 转录因子被证明调控植物细胞内铁稳态，但 bHLH 转录因子之外的调控层面仍不是很清楚。我们证明了 SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE（SPL）TF SlSPL-CNR 负调控番茄（*Solanum lycopersicum*）根系的缺铁反应。铁缺乏迅速抑制了 *SlSPL-CNR* 的表达，并且在两个通过 CRISPR/Cas9 基因编辑技术产生的

SlSPL-CNR 敲除系中，缺铁响应比野生型更强。比较转录组分析发现了 47 个受到 SlSPL-CNR 负调控的缺铁响应基因，其中包括正调控缺铁响应基因表达的 *SlbHLH101* 基因。SlSPL-CNR 定位于细胞核，并与 *SlbHLH101* 启动子中的 GTAC 和 BOX 4 （ATTAAT）元件相互作用以抑制其表达。



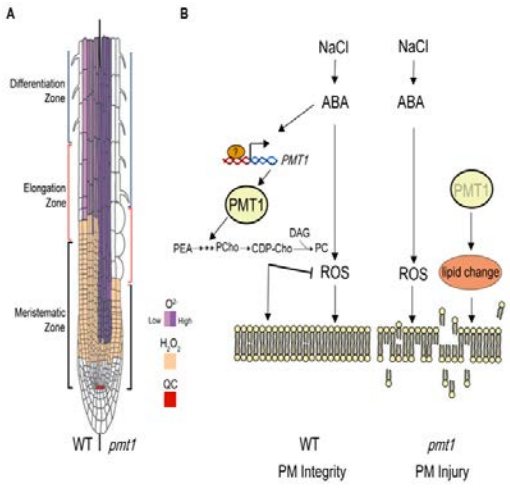
缺铁对 *SlSPL-CNR* 表达的抑制与 microRNA SlymiR157 的表达密切相关。过表达 *SlymiR157* 和 *SlSPL-CNR* 功能缺失突变体一样，均表现为缺铁响应增强。综上，该研究揭示了 SlymiR157-SlSPL-CNR 模块在 SlbHLH101 上游调控番茄根系中的铁稳态（Zhu et al., *J Integr Plant Biol,* 2022）。

The Mir157-SPL-CNR Module Acts Upstream of Bhlh101 to Negatively Regulate Iron Deficiency Responses in Tomato

Iron (Fe) homeostasis is critical for plant growth, development, and stress responses. Fe levels are tightly controlled by intricate regulatory networks in which transcription factors (TFs) play a central role. A series of basic helix‐loop‐helix (bHLH) TFs have been shown to contribute to Fe homeostasis, but the regulatory layers beyond bHLH TFs remain largely unclear. Here, we demonstrate that the SQUAMOSA PROMOTER‐BINDING PROTEIN‐LIKE (SPL) TF SlSPL‐CNR negatively regulates Fe‐deficiency responses in tomato (Solanum *lycopersicum*) roots. Fe deficiency rapidly repressed the expression of *SlSPL‐CNR*, and Fe deficiency responses were intensified in two clustered regularly interspaced palindromic repeats (CRISPR)/CRISPR associated protein 9‐generated SlSPL‐CNR knockout lines compared to the wild‐type. Comparative transcriptome analysis identified 47 Fe deficiencyresponsive genes the expression of which is negatively regulated by SlSPL‐CNR, one of which, *SlbHLH101*, helps regulate Fe uptake genes. SlSPLCNR localizes the nucleus and interacts with the GTAC and BOX 4 (ATTAAT) motifs in the *SlbHLH101* promoter to repress its expression. Inhibition of SlSPL‐CNR expression in response to Fe deficiency was well correlated with the expression of the microRNA SlymiR157. *SlymiR157*‐overexpressing tomato lines displayed enhanced Fe deficiency responses, as did SlSPL‐CNR loss‐of‐function mutants. We propose that the SlymiR157‐SlSPL‐CNR module represents a novel pathway that acts upstream of SlbHLH101 to regulate Fe homeostasis in tomato roots.

4、脱落酸依赖的 *PMT1* 的表达通过缓解脱落酸介导的 ROS 的产生调节拟南芥耐盐性

磷酸胆碱（PCho）是植物非质体膜的中间代谢产物，在植物耐盐性中起重要作用。然而，PCho 代谢调节盐胁迫反应的机制尚不清楚。我们利用 T-DNA 插入突变体、基因编辑等位基因和基因功能恢复株系，研究了磷酸乙醇胺 *N*-甲基转移酶 1（*PMT1*）在拟南芥耐盐中的作用。*pmt1* 突变体在盐胁迫下表现出严重的根系伸长抑制，但外源 ChoCl 或卵磷脂可以恢复这一缺陷。*pmt1* 在盐胁迫下也表现出甘油脂代谢的改变，表明甘油脂代谢参与植物对盐胁迫的耐受性。此外，与野生型幼苗相比，*pmt1* 突变体改变了活性氧（ROS）的积累和分布，降低了细胞分裂活性，并干扰了生长素在主根中的分布。进一步研究表明，*PMT1* 的表达受盐胁迫诱导，并且依赖于脱落酸（ABA）信号通路。在 *aba2-1* 和 *pyl112458* 突变体中，盐诱导 *PMT1* 表达被抑制。同时发现，ABA 通过干扰根尖内 ROS 的分布，加剧了 *pmt1* 突变体的盐敏感性。综上所述，研究证明 PMT1 是一种重要的磷酸乙醇胺 *N*-甲基转移酶，通过 ABA 信号来平衡活性氧的产生和分布，调节盐胁迫下的主根伸长（He et al., *J Integr Plant Biol*, 2022）。



Abscisic Acid-Dependent *PMT1* Expression Regulates Salt Tolerance by Alleviating Abscisic Acid-Mediated ROS Production in *Arabidopsis*

Phosphocholine (PCho) is an intermediate metabolite of nonplastid plant membranes that is essential for salt tolerance. However, how PCho metabolism modulates response to salt stress remains unknown. Here, we characterize the role of phosphoethanolamine *N*-methyltransferase 1 (PMT1) in salt stress tolerance in *Arabidopsis thaliana* using a T-DNA insertional mutant, gene-editing alleles, and complemented lines. The *pmt1* mutants showed a severe inhibition of root elongation when exposed to salt stress, but exogenous ChoCl or lecithin rescued this defect. *pmt1* also displayed altered glycerolipid metabolism under salt stress, suggesting that glycerolipids contribute to salt tolerance. Moreover, *pmt1* mutants exhibited altered reactive oxygen species (ROS) accumulation and distribution, reduced cell division activity, and disturbed auxin distribution in the primary root compared to wild-type seedlings. We show that *PMT1* expression is induced by salt stress and relies on the abscisic acid (ABA) signaling pathway, as this induction was abolished in the *aba2-1* and *pyl112458* mutants. However, ABA aggravated the salt sensitivity of the *pmt1* mutants by perturbing ROS distribution in the root tip. Taken together, we propose that PMT1 is an important phosphoethanolamine *N*-methyltransferase participating in root development of primary root elongation under salt stress conditions by balancing ROS production and distribution through ABA signaling (He et al., *J Integr Plant Biol*, 2022).

（二） 研究成果

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

1. Gao L, Liu X, Gao K, Cui M, Zhu H, Li G, Yang J, Wu Y, **Ding Z**, Chen X, Ma J, Harberd N, **Zheng S*** (2022) ART1 and putrescine contribute to rice aluminum resistance via OsMYB30 in cell wall modification. ***J Integr Plant Biol*** Accepted.
2. Su NN, Zhu A, Tao X, **Ding Z**, Chang S, Ye F, Zhang Y, Zhao C, Chen Q, Wang J, Zhou CY, GuoY, Jiao S, Zhang S, Wen H, Ma L, Ye S, **Zheng S**, Yang F*, Wu S*, Guo J* (2022) Structures and mechanisms of the *Arabidopsis* auxin transporter PIN3. ***Nature*** 609: 616-621.
3. Liu X, Gao L, She B, Li G, Wu Y, **Xu J**, **Ding Z**, Ma J, **Zheng S*** (2022) A novel kinase subverts Aluminum resistance by boosting Ornithine decarboxylase-dependent putrescine biosynthesis. ***Plant Cell Environ*** 45: 2520-2532.
4. He Q, Jin J, Lou H, Dang F, **Xu J**, **Zheng S**, **Yang J*** (2022) Abscisic acid-dependent PMT1 expression regulates salt tolerance by alleviating abscisic acid-mediated reactive oxygen species production in *Arabidopsis*. ***J Integr Plant Biol*** 64: 1803-1820.
5. Zhu H, Wang J, Jiang D, Hong Y, **Xu J**, **Zheng S**, **Yang J***, Chen W* (2022) The miR157-SPL-CNR module acts upstream of bHLH101 to negatively regulate iron deficiency responses in tomato. ***J Integr Plant Biol*** 64: 1059-1075.
6. Wei Y, Yuan J, Xiao C, Li G, Yan J, **Zheng S**, **Ding Z*** (2022) RING-box proteins regulate leaf senescence and stomatal closure via repression of ABA transporter gene ABCG40. ***J Integr Plant Biol*** 64: 979-994.
7. Wen Y, Wang J, Zhu H, Han G, Huang R, Huang L, Hong Y, **Zheng S**, **Yang J***, Chen W* (2022) Potential role of domains rearranged methyltransferase 7 in starch and chlorophyll metabolism to regulate leaf senescence in tomato. ***Front Plant Sci*** doi: 10.3389/fpls.2022.836015.
8. Liu X, Zhang H, Zhu Q, Ye J, Zhu Y, Jing X, Du W, Zhou M, Lin X, **Zheng S**, **Jin C** (2022) Phloem iron remodels root development in response to ammonium as the major nitrogen source. ***Nature Commun*** 13: 561.
9. Wang J[#], Yu [#], **Ding Z**[#], Zhang X, Luo Y, Xu X, Xie Y, Li X, Yuang T, **Zheng S***, Yang W*, Guo J* (2022) Structural basis of ALMT1-mediated aluminum resistance in *Arabidopsis*. ***Cell Res*** 32: 89-98.
10. Jamieson F, Ji Z, Belfield E, **Ding Z**, **Zheng S***, Harberd N* (2022) Ethylene signaling modulates *Arabidopsis thaliana* nitrate metabolism. ***Planta*** 225: 94.

专利申请及授权：

1. 一种拟南芥种子铁累积调控基因 *INO* 及其编码蛋白和应用。申请人：**郑绍建**，孙鹂，李桂新，**丁忠杰**；授权号：ZL202010973235.4；授权日期：2022 年 04 月 15 日。
2. 一种调控植物抗铝性的铝离子受体 *ALR1* 基因或蛋白的应用。申请人：**郑绍建**，**丁忠杰**，徐晨，李桂新；授权号：ZL202110367334.2；授权日期：2022 年 07 月 08 日。

（三） 研究队伍

固定人员：

郑绍建（课题组长），杨建立，丁忠杰。

研究生：

魏运其，徐晨，高丽君，崔孟奇，何琦瑜，徐丽霖，袁俊杰，袁甜，祝慧慧，徐洁娜，姜百惠，王嘉怡，王雅男，李艾凝，马哲宇，文雨昕，王雨璇，高可可，张淼倩，王涛，周晨羽，刘梦淳，赵亚男，季琳凯，周晨羽，岑泽雨，俞苏航，梁裕蕾。

寿惠霞

课题组

寿惠霞，教授。

研究方向：植物营养生理与分子生物学，植物生物技术及作物转基因。

（一） 研究进展

水稻三个液泡磷酸盐转运 SPX-MFS 在磷稳态调控中的功能

磷是确保植物正常生长和产量的重要元素，液泡中的磷储量对植物细胞缓冲环境磷波动非常重要，解析水稻液泡磷酸盐转运体的功能对培育磷高效水稻具有重要意义。本课题组在 2015 年报导了首个植物液泡磷转运体 OsSPX-MFS3（Wang et al., 2015），蛙卵母细胞试验表明 OsSPX-MFS3 具有磷转运活性，而其运输方向取决于外部 pH 值和无机磷的浓度。但当时由于没有相应的突变体材料，无法明确对该液泡膜转运体对无机磷的转运方向。为了澄清上述问题并进一步明确水稻中三个同源基因的功能分工，本研究创制了 *OsSPX-MFS1-3* 三个基因的单突变体、双突变体和三突变体等 7 个突变体组合，详细解析了 OsSPX-MFS1-3 在调控磷酸盐稳态过程中的功能和转运方向。研究表明，除 *Osspx-mfs2* 外的所有突变体均表现出液泡 Pi 浓度下降，而 *OsSPX-MFSs* 过表达植物液泡中的 Pi 过量积累，表明所有 OsSPX-MFSs 都是液泡 Pi 内流转运体。对突变体表型分析发现，OsSPX-MFS3 在三个转运体中起了主导作用；而 OsSPX-MFS2 功能最弱。*Osspx mfs1/3* 和 *Osspx-mfs1/2/3* 突变体的液泡 Pi 储存能力严重受损，导致 Pi 组织分配异常。*Osspx-mfs1/3* 和 *Osspx-mfs1/2/3* 穗中的 Pi 高度积累，损害穗的正常发育和育性。与野生型相比，*Osspx-mfs2* 在田间低磷状态下种植时产量更加稳定。因此，适当调低水稻液泡磷的储存能力，可提高水稻对低磷的耐受性以及磷利用效率。上述研究结果为提高水稻对低磷耐受性以及磷利用效率提出了一条新策略。该研究成果于 2022 年 8 月在《*Plant Cell and Environment*》上发表。

Functional Characterization of the Three Oryza Sativa SPX-MFS Proteins in Maintaining Phosphate Homoeostasis

Plant vacuoles serve as the primary intracellular compartments for phosphorus (P) storage. The Oryza sativa genome contains three genes that encode SPX (SYG1/ PHO81/XPR1) -MFS (Major Facility Superfamily) proteins (OsSPX-MFS1-3). The physiological roles of the three transporters under varying P conditions in laboratory and field are not known. To address this knowledge gap, we generated single, double and triple mutants for three *OsSPX‐MFS* genes. All the mutants except *Osspx-mfs2* display lower vacuolar Pi concentrations and *OsSPX-MFSs*

overexpression plant display higher Pi accumulation, demonstrating that all OsSPX-MFSs are vacuolar Pi influx transporters. OsSPX-MFS3 plays the dominant role based on the phenotypes of single mutants in terms of growth, vacuolar and tissue Pi concentrations. OsSPX-MFS2 is the weakest and only functions as vacuole Pi sequestration in an *Osspx-mfs1/3* background. The vacuolar Pi sequestration capacity was severely impaired in *Osspx-mfs1/3* and *Osspx-mfs1/2/3*, which resulted in increased Pi allocation to aerial organs. High P in the panicle impaired panicle and fertility in *Osspx-mfs1/3* and *Osspx-mfs1/2/3*. *Osspx-mfs2* resulted in a more stable yield compared to the wild type under low Pi in field grown plants. The results suggest that alteration of vacuolar Pi sequestration may be a novel effective strategy to improve rice tolerance to low phosphorus in cropping systems.

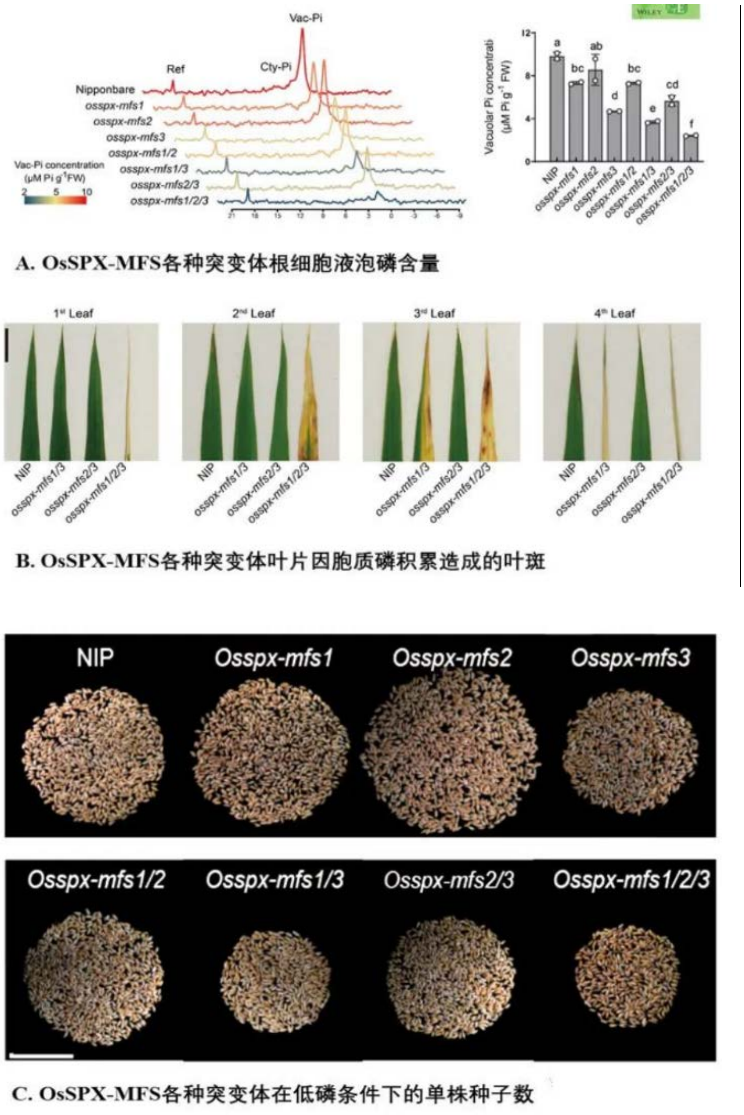


图 1、水稻液泡磷转运体 OsSPX-MFS 在维持磷稳态中的功能。

Figure 1. Function of OsSPX-MFS proteins in maintaining phosphate homoeostasis.

（二） 研究成果

发表论文：（*Corresponding author）

英文期刊论文：

Guo R, Zhang Q, Ying Y, Liao W, Liu Y, Whelan J, **Mao C**, **Shou H*** (2022) Functional characterization of the three Oryza sativa SPX-MFS proteins in maintaining phosphate homeostasis. ***Plant Cell Environ*** https://doi.org/10.1111/pce.14414

专利申请及授权：

pSOY19-ZM2 载体、其制备方法及应用。申请人：**寿惠霞**，朱佳美，李林，王守冬，徐恬恬；授权号：ZL202110526546.0；授权日期：2022 年 06 月 27 日。

（三） 研究队伍

固定人员：

寿惠霞（课题组长），应颖慧。

博士后：

郭润泽，李钦雪。

研究生：

硕士生：杨临泽，方静，高熊枫，刘那。

博士生：张琦，孔琪惠，王瑶，廖文英，郭润泽，朱佳美，李杰，胡珊珊，干乐宁，金梦圆，史琬璇。

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 OsHMG1 改变染色质可及性及基因表达进而调控磷平衡的分子机制

通过缺磷转录组数据筛选到低磷诱导基因 *HMG*，该基因编码一个高速泳动族蛋白。*HMG* 的转录水平和蛋白水平在低磷条件下都会受到诱导。HMG 定位于细胞核，并且在各组织中广泛表达（图 1）。*hmg* 突变体叶片的无机磷浓度显著降低，而超表达材料中的无机磷浓度显著升高，说明 HMG 在水稻体内正调控无机磷浓度（图 1）。通过 RNA-seq 分析发现，有大量的磷饥饿诱导基因（PSIs）和磷饥饿抑制基因（PSSs）的转录水平受到 HMG 调控。ChIP-seq 分析结果表明 HMG 广泛地结合在许多基因的启动子上，包括大部分依赖于 HMG 调控的磷饥饿响应基因。ATAC-seq 分析发现，HMG 会影响全基因组的染色质可及性。相关结果揭示了一种新的调控磷稳态的表观遗传机制：HMG 结合在磷饥饿响应基因的启动子上，通过促进这些基因的染色质可及性增加调控基因表达，进而调控水稻体内磷平衡。

另外，详细总结了水稻响应环境磷饥饿胁迫的分子机制、根系感知环境磷水平改变根构型以提高磷吸收、转运及再分配的分子机制，讨论了水稻磷高效利用性状遗传改良的实践策略并提出了今后的研究方向（Lu et al., *Plant Cell Environ*, 2022）。

Revealed the Molecular Mechanism of Oshmg1 Regulating Phosphate Homeostasis by Altering Chromatin Accessibility and Gene Expression

The phosphate inducible gene *OsHMG1* was identified based on phosphate-deficient transcriptome, which encodes a high mobility group protein. Both the transcript and protein levels of *OsHMG1* are induced under low phosphorus conditions. OsHMG1 is localized in the nucleus and widely expressed in different tissues (Figure 1). The inorganic phosphate concentration in the leaves of the *hmg* mutant significantly decreased, while the inorganic phosphate concentration in the overexpressed material significantly increased, indicating that OsHMG1 positively regulates the inorganic phosphate concentration in rice (Figure 1). By RNA-seq analysis, it was found that the transcript levels of a large number of phosphate starvation induced genes (PSIs) and phosphate starvation suppressed genes (PSSs) were regulated by HMG. The results of ChIP-seq analysis showed that HMG is extensively bound to the promoters of many genes, including most phosphate-starvation responsive genes. ATAC-seq analysis incidated that HMG affected

genome-wide chromatin accessibility. The related results reveal a novel epigenetic mechanism for regulating phosphate homeostasis: HMG binds to the promoter of phosphate starvation response genes, and increases the gene expression by promoting chromatin accessibility of these genes, thereby regulates phosphate homeostasis in rice.

In addition, the molecular mechanism of rice response to environmental phosphate starvation and the molecular mechanism of root sensing of environmental phosphorus level and changing root architecture to improve phosphate uptake, transport and redistribution were summarized in detail. The practical strategies for genetic improvement of phosphate efficient utilization traits in rice were discussed and the future research directions were proposed (Lu et al., *Plant Cell Environ*, 2022).

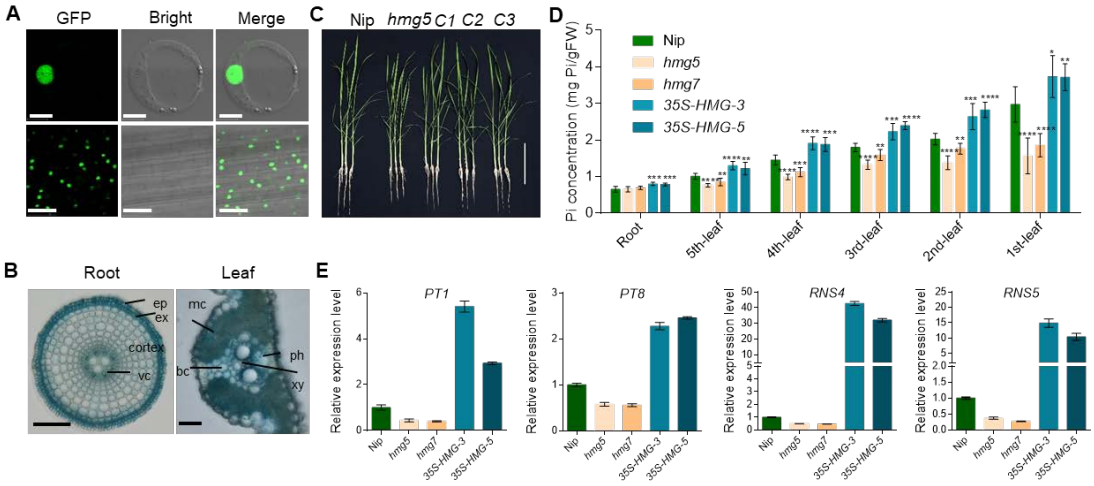


图 1、OsHMG 的组织表达、亚细胞定位及其突变体和增强表达材料的表型。

Figure 1. The tissue specific expression, subcellular localization of OsHMG1 and the phenotype of its mutant and overexpression lines.

2、水稻中 LFNR 膜锚定特性的研究

高等植物叶型铁氧还蛋白-NADP⁺氧化还原酶 LFNR（Leaf-type Ferredoxin–NADP⁺ oxidoreductase）负责催化光合线性电子传递的最后一步反应，催化电子由还原态的铁氧还蛋白（Fd）传递给 $NADP^+$。生成的还原力 NADPH 主要用于卡尔文循环中 CO_2 的固定和叶绿体的其他代谢过程。在拟南芥中，LFNR 可以通过与膜锚定蛋白 TIC62 或 TROL 结合，从而紧密结合于类囊体膜与叶绿体内膜上。此外，基质中还存在着未与膜锚定蛋白发生结合的可溶性 LFNR 能够直接较弱的和类囊体结合。对于正常生长条件下的光合作用来说，LFNR 膜锚定并不是必需的，但是 LFNR 膜锚定却呈现光下解离，黑暗中锚定到膜上的规律，膜锚定的 LFNR 有何生理意义还并不是很清楚，此外，相比于拟南芥中 LFNR 的膜锚定特性已经比较清楚，但是在水稻中还有许多空白。我们的研究结果表明：在水稻中，LFNR 也需要与膜锚定蛋白结合从而紧密结合于类囊体膜与叶绿体内膜上。OsTIC62 介导锚定的是类囊体膜上紧密结合的高分子量 LFNR 复合物，而低分子量 LFNL 复合物则

依赖于 OsTROL1 介导锚定，中分子量 LFNF 复合物可能是 OsTROL2-OsLFNR 和 OsTIC62-OsLFNR 的混合物。其次，OsLFNRs 与膜锚蛋白之间彼此存在着相互促进稳定的作用。同时，膜锚定蛋白 OsTROL1 的缺失会导致另一个膜锚定蛋白 OsTIC62 的代偿性增加。另一个有趣的现象是，在 *Oslfnr2* 突变体中，OsLFNR 锚定复合物从类囊体膜上消失，而 *Oslfrn1* 中仍然有许多 OsLFRN 锚定复合物，这表明 OsLFNN1 与类囊体锚定蛋白的结合需要依赖于 OsLFNL2。这与拟南芥报道的 LFNR2 依赖于 LFNR1 锚定到类囊体膜上的结果刚好相反，体现出物种差异。此外，与拟南芥中类囊体膜无 LFNR 锚定结合突变体（*tic62 trol1*）不影响正常条件下的生长及光合作用速率不同，水稻中类囊体膜上锚定的各 LFNR 复合体对维持较高光合同化能力是发挥一定功能的；最后，课题组发现 OsTIC62 在夜间比白天有更高表达的昼夜节律，这一发现又增加了新的 LFNR 的光控锚定机制（Da et al., *Plant Cell Environ*, 2022）。

Characterizing Membrane Anchoring of Leaf - Form Ferredoxin - $NADP^+$ Oxidoreductase in Rice

Leaf-form ferredoxin-$NADP^+$ oxidoreductcropases (LFNRs) function in the last step of the photosynthetic electron transport chain, exist as soluble proteins in the chloroplast stroma and are weakly associated with thylakoids or tightly anchored to chloroplast membranes. *Arabidopsis* thaliana has two LFNRs, and the chloroplast proteins AtTROL and AtTIC62 participate in anchoring AtLFNRs to the thylakoid membrane. By contrast, the membrane anchoring mechanism of rice (*Oryza sativa*) LFNRs has not been elucidated. Here, we investigated the membrane-anchoring mechanism of LFNRs and its physiological roles in rice. We characterized the rice protein OsTROL1 based on its homology to AtTROL. We determined that OsTROL1 is also a thylakoid membrane anchor and its loss leads to a compensatory increase in OsTIC62. OsLFNR1 attachment through a membrane anchor depends on OsLFNR2, unlike the *Arabidopsis* counterparts. In addition, OsTIC62 was more highly expressed in the dark than under light conditions, consistent with the increased membrane binding of OsLFNR in the dark. Moreover, we observed reciprocal stabilization between OsLFNRs and their membrane anchors. In addition, unlike in *Arabidopsis*, the loss of LFNR membrane anchor affects photosynthesis in rice. Overall, our study sheds light on the mechanisms anchoring LFNRs to membranes in rice and highlights differences with *Arabidopsis* (Da et al., *Plant Cell Environ*, 2022).

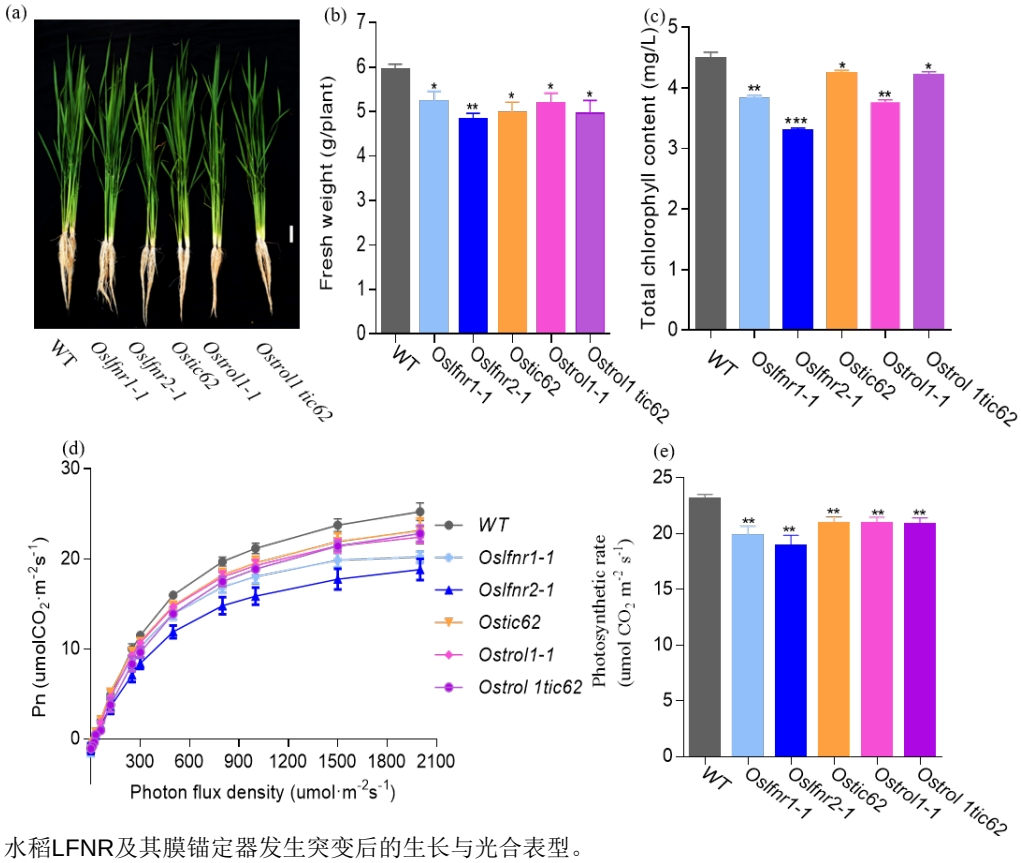


图2、水稻LFNR及其膜锚定器发生突变后的生长与光合表型。

Figure 2. Mutation of OsLFNRs and their putative anchors affects growth and photosynthesis.

3、泛素水解酶 2（OsUBP2）负调控水稻细胞程序性死亡与抗病的研究

类病变突变体（LMMs）是研究细胞程序性死亡与免疫机制的植物材料，我们鉴定了一个水稻锈斑突变体 *rsr1*，它具有类病斑表型与活性氧的积累，同时还表现出增强稻瘟病与白叶枯的抗性；通过图位克隆我们揭示了 *RSR1* 编码泛素水解酶 2 基因（*OsUBP2*）；超表达 *OsUBP2* 水稻植株表现出抗病性减弱，说明 OsUBP2 是活性氧积累与抗病性的负调控因子；OsUBP2 在体外具有泛素水解酶活性，通过对野生型与 *rsr1* 突变体的泛素化蛋白质组学的比较，我们提出了一些潜在的 OsUBP2 靶蛋白候选（Jang et al., *Plants*, 2022）。

Ubiquitin-Specific Protease 2 (OsUBP2) Negatively Regulates Cell Death and Disease Resistance in Rice

Lesion mimic mutants (LMMs) are great materials for studying programmed cell death and immune mechanisms in plants. Various mechanisms are involved in the phenotypes of different LMMs, but few studies have explored the mechanisms linking deubiquitination and LMMs in rice (*Oryza sativa*). Here, we identified a rice LMM, *rust spots rice* (*rsr1*), resulting from the mutation of a single recessive gene. This LMM has spontaneous reddish-brown spots on its leaves, and displays enhanced resistance to both fungal leaf blast (caused by *Magnaporthe oryzae*) and

bacterial blight (caused by *Xanthomonas oryzae* pv. *oryzae*). Map-based cloning showed that the mutated gene in *rsr1* encodes a *Ubiquitin-Specific Protease 2* (*OsUBP2*). The mutation of *OsUBP2* was shown to result in reactive oxygen species (ROS) accumulation, chloroplast structural defects, and programmed cell death, while the overexpression of *OsUBP2* weakened rice resistance to leaf blast. OsUBP2 is therefore a negative regulator of immune processes and ROS production. OsUBP2 has deubiquitinating enzyme activity in vitro, and the enzyme active site includes a cysteine at the 234th residue. The ubiquitinated proteomics data of *rsr1* and WT provide some possible target protein candidates for OsUBP2 (Jang et al., *Plants*, 2022).

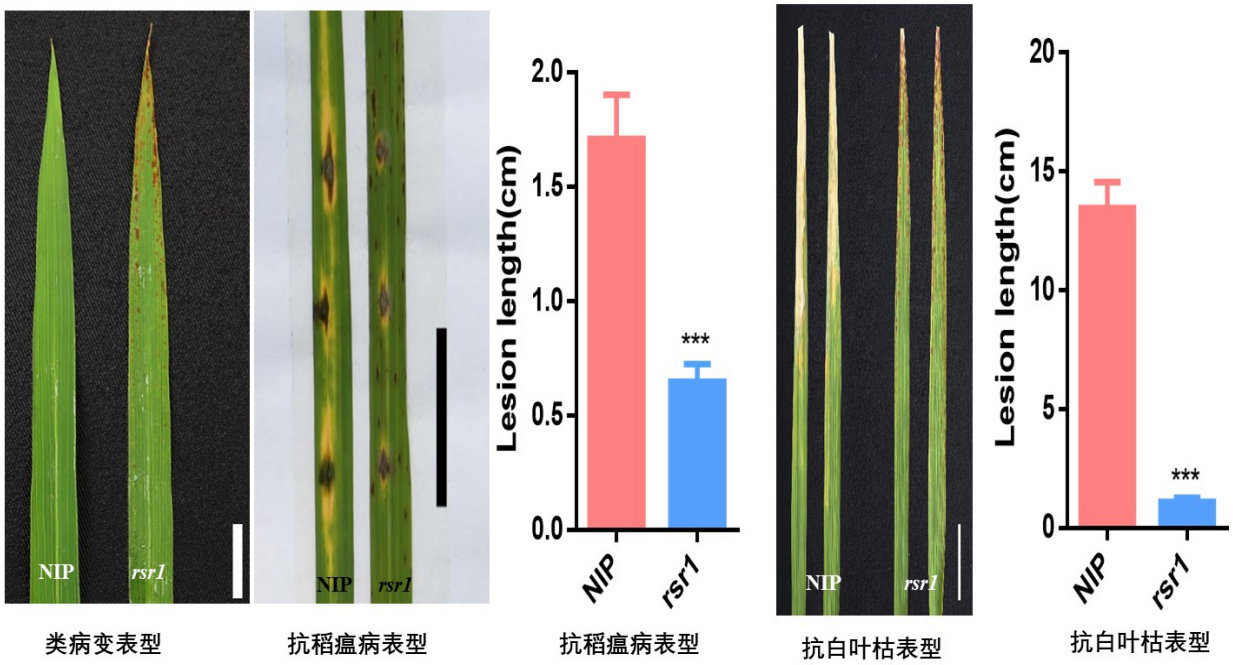


图3、类病斑突变体*rsr1*具有增强稻瘟病与白叶枯抗性的表型。

Figure 3. *rsr1* mutant has spontaneous reddish-brown spots on its leaves, and displays enhanced resistance to both fungal leaf blast (caused by *Magnaporthe oryzae*) and bacterial blight (caused by *Xanthomonas oryzae* pv. *oryzae*).

（二） 研究成果

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

1. Da X, Guo J, Yan P, Yang C, Zhao H, Li W, Kong Y, Jiang R, He Y, **Xu J**, Xu O, **Mao C**, **Mo X*** (2022) Characterizing membrane anchoring of leaf-form ferredoxin-NADP (+) oxidoreductase in rice. ***Plant Cell Environ*** doi:10.1111/pce.14446.
2. Li Y, Wu L, Ren M, Zhu J, **Xu J**, Hu H, Quan X, Huang C, **Mao C*** (2022) Functional redundancy of *OsPIN1* paralogous genes in regulating plant growth and development in rice. ***Plant Signal Behav*** 17: 2065432.
3. Lu H, Wang F, Wang Y, Lin R, **Wang Z**, **Mao C*** (2022) Molecular mechanisms and genetic

improvement of low-phosphorus tolerance in rice. ***Plant Cell Environ*** doi:10.1111/pce.14457.

4. Jiang R, Zhou S, Da X, Chen T, **Xu J**, Yan P, **Mo X*** (2022) Ubiquitin-specific protease 2 (OsUBP2) Negatively regulates cell death and disease resistance in rice. ***Plants*** 11. 2568.

专利申请及授权：

1. OsbHLH6 在提高作物磷吸收能力及作物耐低磷育种中的应用。申请人：**毛传澡**，何秋菊，**莫肖蓉**，**徐纪明**；授权号：202010779838.0；授权日期：2022 年 03 月 14 日。
2. 水稻根分泌多肽 PEP1 及其编码基因和应用。申请人：**毛传澡**，蒙福宁，向丹，王奥迪；授权号：202110194477.8；授权日期：2022 年 05 月 27 日。
3. OsWRKY12 及其在水稻磷高效育种中的应用。申请人：**毛传澡**，毛文轩，**徐纪明**；授权号：202011618909.5；授权日期：2022 年 03 月 22 日。
4. 一种蛋白磷酸酶 OsPP74 在提高水稻磷吸收中的应用。申请人：**毛传澡**，邓美菊，王飞，**徐纪明**；授权号：202011591443.4；授权日期：2022 年 06 月 20 日。

（三） 研究队伍

固定人员：

毛传澡（课题组长），莫肖蓉，吴忠长，徐纪明，刘于。

博士后：

朱建树，李勇，王飞，任美燕。

研究生：

陆宏，姜瑞瑞，李梦真，王奥迪，王燕，周洪竹，郭梦雪，李伟，王凯，黄骆彬，邓美菊，林荣斌，刘佳明，应卢迎，吴坤晓，刘溢健，赵科举，笪潇文，严鹏，周诗晨。

金崇伟

课题组

金崇伟，教授。

研究方向：植物营养逆境胁迫耐受机制。

（一） 研究进展

韧皮部质外体铁积累在铵胁迫抑制植物根系生长中的作用及机制

氮是植物生长必需的大量元素，其中铵态氮和硝态氮是植物主要利用的无机氮源，但以铵态氮为主要氮源或唯一氮源时，植物生长会表现出严重的毒害现象。其中，根系生长抑制是植物铵毒的典型症状。我们的研究在拟南芥中的研究表明，无论是突变细胞壁定位的铁氧化酶 LPR2，还是减少铁供应，都能有效缓解铵胁迫对主根生长的抑制。进一步研究表明，与硝态氮相比，铵态氮在韧皮部外质体中以 LPR2 依赖的方式导致过量铁的积累。这种异常的铁积累随后导致大量的胼胝质沉积在韧皮部，从而导致活性氧的爆发，最终破坏韧皮部的功能。因此，铵胁迫使韧皮部的蔗糖运输和卸载都受到显著抑制，从而导致主根生长区的细胞蔗糖供应不足，成为主根生长抑制的直接原因。该发现为解决农业生态系统或自然植被生态保护中的铵毒害问题提供了新的理论依据和研究思路（Liu et al., *Nat Commun*, 2022）。

The Role of Phloem Iron in Root Growth Inhibition by Ammonium Stress and Its Underlying Mechanisms

Plants use nitrate and ammonium as major nitrogen (N) sources, each affecting root development through different mechanisms. However, the exact signaling pathways involved in root development are poorly understood. Here, we show that, in *Arabidopsis thaliana*, either disruption of the cell wall-localized ferroxidase LPR2 or a decrease in iron supplementation efficiently alleviates the growth inhibition of primary roots in response to NH^{4+} as the N source. Further study revealed that, compared with nitrate, ammonium led to excess iron accumulation in the apoplast of phloem in an LPR2-dependent manner. Such an aberrant iron accumulation subsequently causes massive callose deposition in the phloem from a resulting burst of reactive oxygen species, which impairs the function of the phloem. Therefore, ammonium attenuates primary root development by insufficiently allocating sucrose to the growth zone. Our results link phloem iron to root morphology in response to environmental cues (Liu et al., *Nat Commun*, 2022).

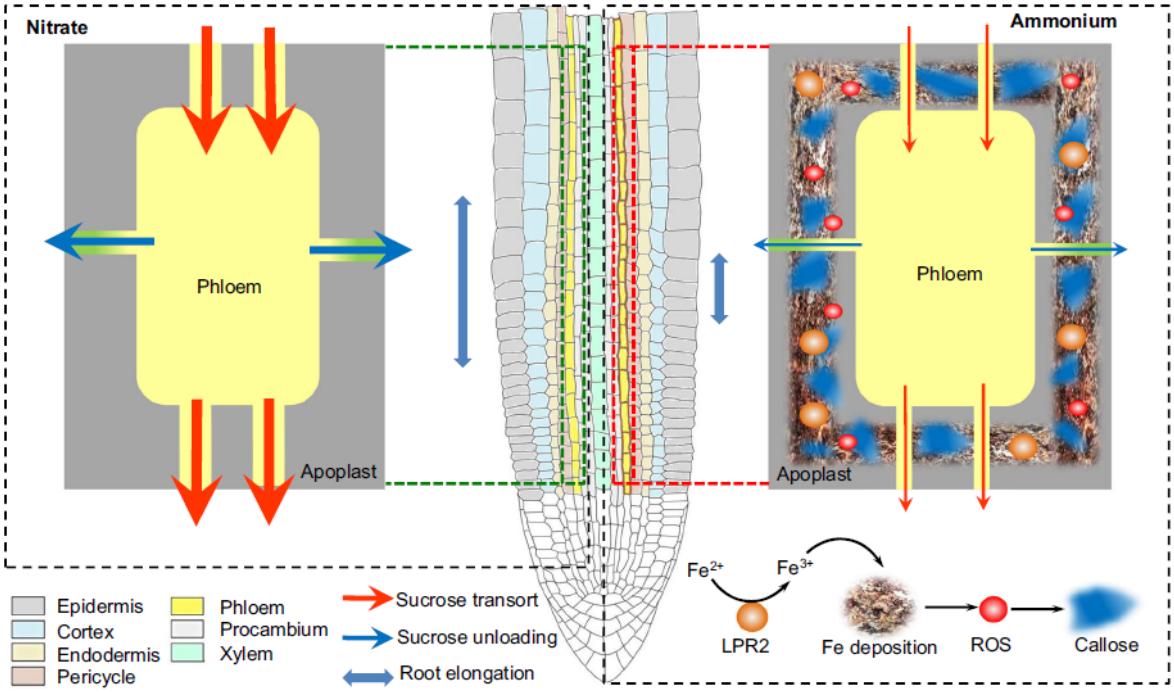


图 1、LPR2 介导的韧皮部质外体铁沉积在铵胁迫抑制根系生长中的作用机制模式图。

Figure 1. Schematic model of the mechanism that connects remodeling of root development to NH_4^+ as the primary N source.

（二） 研究成果

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

Liu X, Zhang H, Zhu Q, Ye J, Zhu Y, Jing X, Du W, Zhou M, Lin X, **Zheng S**, **Jin C*** (2022) Phloem iron remodels root development in response to ammonium as the major nitrogen source. ***Nature Commun*** 13: 563.

（三） 研究队伍

固定人员：

金崇伟（课题组长）。

研究生：

祝亚昕，刘星星，叶佳园，杜闻昕，朱清扬，周苗。

刘建祥课题组

刘建祥，教授。

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

RVE5 协调生物钟与温和高温下植物生长的竞争-衰减分子机制

全球变暖对植物生长和发育有着深远的影响，植物不断调整其内部生物钟以应对外部环境。然而，与时钟相关的基因如何微调植物的温度响应和生长却鲜为人知。我们发现 *REVEILLE5*（*RVE5*）功能缺失突变降低了拟南芥中昼夜节律基因 *EARLY FLOWERING 4*（*ELF4*）的表达，导致温和高温条件下植物下胚轴的生长加快。RVE5 和 CIRCADIAN CLOCK ASSOCIATED 1（CCA1）都在温和高温下积累，并与 *ELF4* 启动子上的相同 EE 顺式元件结合，但 RVE5 的转录抑制活性弱于 CCA1，并且在 *rve5-2* 突变体背景中过表达 *ELF4* 抑制了温和高温下的 *rve5-2* 突变表型。因此，转录抑制因子 RVE5 通过在温和高温下与更强的转录抑制因子 CCA1 在顺式元件上竞争来微调 *ELF4* 的表达。这种竞争-衰减机制提供了一个平衡系统，用于在温和高温下调节 *ELF4* 的表达水平和热响应的下胚轴生长（Li et al., *New Phytol*, 2022）。

A Competition-Attenuation Mechanism Modulates Thermoresponsive Growth at Warm Temperatures in Plants

Global warming has profound impact on growth and development, and plants constantly adjust their internal circadian clock to cope with external environment. However, how clock-associated genes fine-tune thermoresponsive growth in plants is little understood. We found that loss-of-function mutation of *REVEILLE5* (*RVE5*) reduces the expression of circadian gene *EARLY FLOWERING 4* (*ELF4*) in *Arabidopsis*, and confers accelerated hypocotyl growth under warm-temperature conditions. Both RVE5 and CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) accumulate at warm temperatures and bind to the same EE *cis*-element presented on *ELF4* promoter, but the transcriptional repression activity of RVE5 is weaker than that of CCA1. The binding of CCA1 to *ELF4* promoter is enhanced in the *rve5-2* mutant at warm temperatures, and overexpression of *ELF4* in the *rve5-2* mutant background suppresses the *rve5-2* mutant phenotype at warm temperatures. Therefore, the transcriptional repressor RVE5 finetunes *ELF4* expression via competing at a *cis*-element with the stronger transcriptional repressor CCA1 at warm temperatures. Such a competition–attenuation mechanism provides a balancing system for

modulating the level of ELF4 and thermoresponsive hypocotyl growth under warm-temperature conditions (Li et al., *New Phytol*, 2022).

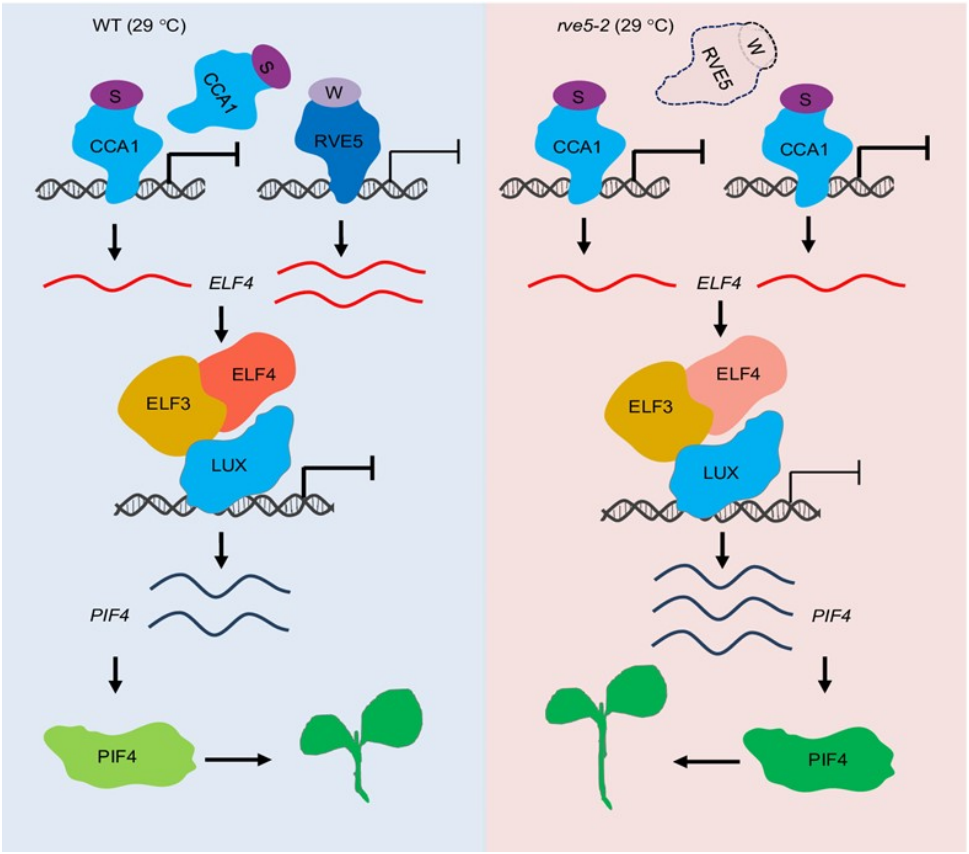


图1、RVE5通过调节*ELF4*基因表达调控温和高温下植物下胚轴生长的竞争-衰减分子模型。

Figure 1. A competition-attenuation working model for modulating *EARLY FLOWERING 4*（*ELF4*）expression and thermoresponsive hypocotyl growth.

（二） 研究成果

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

1. Li W, Tian Y, Li J, Yuan L, Zhang L, Wang Z, Xu X, Davis S, **Liu J*** (2022) A competition-attenuation mechanism modulates thermoresponsive growth at warm temperatures in plants. ***New Phytol*** 237: 177-191.
2. Tian Y, Li W, Wang M, Li J, Davis S, **Liu J*** (2022) REVEILLE 7 inhibits the expression of the circadian clock gene *EARLY FLOWERING 4* to fine-tune hypocotyl growth in response to warm temperatures. ***J Integr Plant Biol*** 64: 1310-1324.

3. Song Z, Chen X, Luo L, Yu F, **Liu J***, Han J* (2022) UBA domain protein SUF1 interacts with NatA-complex subunit NAA15 to regulate thermotolerance in *Arabidopsis*. ***J Integr Plant Biol*** 64: 1297-1302.
4. Li J, Yang C, Tian Y, **Liu J*** (2022) Regulation of chloroplast development and function at adverse temperatures in plants. ***Plant Cell Physiol*** 63: 580-591.
5. Li J, Sun J, Tian Y, **Liu J*** (2022) The FtsH-inactive protein FtsHi5 is required for chloroplast development and protein accumulation in chloroplasts at low ambient temperature in *Arabidopsis*. ***Front Plant Sci*** 12: 830390.
6. Lyu Y, Cao , Huang W, **Liu J***, Lu H* (2022) Disruption of three polyamine uptake transporter genes in rice by CRISPR/Cas9 gene editing confers tolerance to herbicide paraquat. ***aBIOTECH*** 3: 140-145.
7. Lu H, Wang J, Wang M, **Liu J*** (2022) Roles of plant hormones in thermomorphogenesis. ***Stress Biol*** 1: 20.
8. Gao J, Wang M, Wang J, Lu H, **Liu J*** (2022) bZIP17 regulates heat stress tolerance at reproductive stage in *Arabidopsis*. ***aBIOTECH*** 3: 1-11.
9. Li J, **Liu J*** (2022) TT3.1: a journey to protect chloroplasts upon heat stress. ***Stress Biol*** 2: 27.
10. Zhou Y, Qing T, Shu X*, **Liu J*** (2022) Unfolded protein response and storage product accumulation in rice grains. ***Seed Biol*** 1: 7.
11. Peng L*, Gu T, Xu Y, Dad H, **Liu J**, Lian J, Huang L* (2022) Gene delivery strategies for therapeutic proteins production in plants: emerging opportunities and challenges. ***Biotech Adv*** 54: 107845.
12. Lu H, Gao Q, Han J, Guo X, Wang Q, Altosaar L, Barberon M, **Liu J**, Gatehouse A*, Shu Q* (2022) An ABA-serotonin module regulates root suberization and salinity tolerance. ***New Phytol*** 236: 958-973.

专利申请及授权：

时钟基因 *RVE*5 在调控植物生长和开花时间中的应用。申请人：**刘建祥**，李伟；授权号：ZL202111098837.0；授权日期：2022 年 10 月 08 日。

（三） 研究队伍

固定人员：

刘建祥（课题组长），芦海平。

博士后：

李劲宇，王梅敬。

研究生：

田莹莹，邵宇坚，李伟，吕昱树，姚紫薇，祝巧云，张霖霖，杨闯，卿涛，王晶晶，高娟，罗安妮，谢天赐，朱栋杰，王誉晓。

王智烨课题组

王智烨，研究员。

研究方向：植物养分逆境胁迫响应的分子机制及农作物养分高效改良。

（一） 研究进展

水稻全基因组体内 RNA 二级结构检测方法优化

近几年，体内RNA二级结构生物学功能研究的快速发展得益于体内RNA结构检测技术的不断进步。相比于模式植物拟南芥，农作物体内RNA二级结构的功能研究还很少。这其中一个主要原因是缺少针对农作物材料优化的体内RNA结构检测方法。DMS-MaPseq是目前最为常用的体内RNA二级结构检测方法之一。该方法结合DMS化学修饰和高通量测序技术。我们在DMS处理浓度和高通量测序建库方面进行了改进，得到了高质量的水稻不同组织的RNA二级结构数据。进一步，我们利用优化的方法发现了一个潜在的水稻缺磷响应调控RNA结构位点（图1）。该研究有助于水稻RNA二级结构功能的研究，为深入研究RNA二级结构参与的水稻缺素胁迫响应提供了重要的方法基础（Jin et al., *Front Plant Sci*, 2022）。这个优化方法很快应用到南京农业大学范晓荣老师课题组的研究中，帮助其解析了*OsNRT2.3*介导的水稻高产和高氮素利用的新机制（Zhang et al., *Sci Adv*, 2022）。

此外，我们受邀与国内外专家共同在SCIENCE CHINA Life Science期刊撰写动植物RNA结构研究进展综述。在这篇综述中，我总结了植物RNA二级结构在非生物胁迫响应中的功能研究进展，并展望了RNA结构导向的农作物改良（Xu et al., *Sci China Life Sci*, 2022）。同时，我也受邀和毛传澡教授一起在*Plant Cell & Environment*期刊撰写综述，总结水稻耐受低磷环境胁迫的分子机制及遗传改良（Lu et al., *Plant Cell Environ*, 2022）。

Optimization of Genome-Wide RNA Secondary Structure Probing Method in Rice

With the development of in vivo RNA structure probing technologies, growing evidence show important biological functions of RNA secondary structure (RSS) recently. Compared to *Arabidopsis*, the study of RSS in crop is limited. One limitation is no RSS probing method optimized for crop materials. DMS-MaPseq is one of currently used in vivo RSS probing methods, coupling DMS modification with next-generation sequencing (NGS). We optimized DMS treatment conditions and NGS library construction, obtaining hight-quality RNA structure data for various rice tissues. Furthermore, using our optimized method, we found a potential RNA structure region

participating in rice phosphate-starvation responses (Figure 1). This study provided an optimized in vivo RSS probing method for rice, facilitating the study of RNA structure-mediated biological funtions in rice (Jin et al., *Front Plant Sci*, 2022). Notably, this method had been used in Prof. Xiaorong Fan's study and revealed a new mechanism of *OsNRT2.3*-mediated high yield and high-efficient nitrogen usage in rice (Zhang et al., *Sci Adv*, 2022).

Additionally, we were invited by SCIENCE CHINA Life Science to write a comprehensive review of RNA structure functions in animals and plants with other experts. In this review, I summarized the advance of RNA structure functions in plant abiotic stress responses and prospeted RNA structure-guided crop improvement (Xu et al., *Sci China Life Sci*, 2022). Prof. Chuanzao Mao and me were also invied by *Plant Cell & Environment* to write a review summarizing the mechanisms of low-phosphorus stress responses and genetic improvement in rice (Lu et al., *Plant Cell Environ*, 2022).

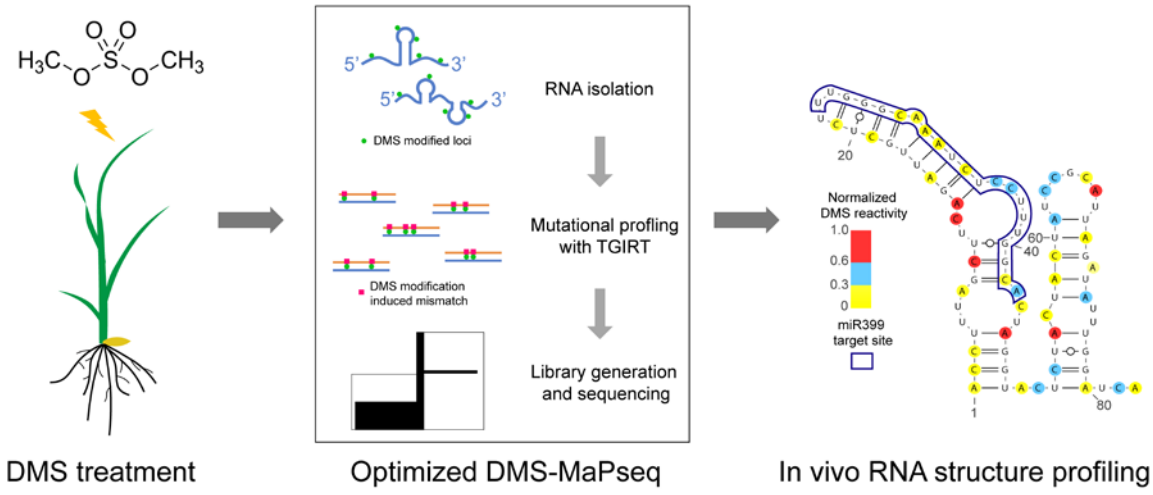


图 1、水稻全基因组 RNA 二级结构检测方法优化。

Figure 1. Optimized genome-wide in vivo RNA secondary structure porbing in rice.

（二） 研究成果

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

1. Jin Q, Zhang L, Hu S, Wei G, **Wang Z*** (2022) Probing in vivo RNA structure with optimized DMS-MaPseq in rice. ***Front Plant Sci*** 13: 869267.

2. Xu B#, Zhu Y#, Cao C#, Chen H#, Jin Q#, Li G#, Ma J#, Yang SL#, Zhao J#, Zhu J#, Ding Y*, Fang X*, Jin Y*, Kwok CK*, Ren A*, Wan Y*, **Wang Z***, Xue Y*, Zhang H*, Zhang QC*, Zhou Y* (2022) Recent advances in RNA structurome. ***Sci China Life Sci*** 65: 1285-1324.

3. Lu H, Wang F, Wang Y, Lin R, **Wang Z***, **Mao C*** (2022) Molecular mechanisms and genetic

improvement of low-phosphorus tolerance in rice. ***Plant Cell Environ*** PMID: 36208118.

4. Zhang Y, Tateishi-Karimata H, Endoh T, Jin Q, Li K, Fan X, Ma Y, Gao L, Lu H, **Wang Z**, Cho AE, Yao X, Liu C, Sugimoto N, Guo S, Fu X, Shen Q, Xu G, Herrera-Estrella LR, Fan X (2022) High-temperature adaptation of an OsNRT2.3 allele is thermoregulated by small RNAs. ***Sci Adv*** 8:eadc9785.

（三） 研究队伍

固定人员：

王智烨（课题组长）。

博士后：

乔露露，李兵杰，董伟国。

研究生：

金琼莉，柳凯，王婧怡，郑方舟，魏广博，胡赛燕，王淑蔓，高睿仁。

徐　娟

课题组

徐娟，教授。

研究方向：植物生长发育及抗逆的分子信号调控机制。

（一） 研究进展

揭示了基质金属蛋白酶 MMP 在拟南芥叶片衰老调控中的新功能

植物叶片衰老是一个发育性的程序性细胞死亡过程，受到各种内源信号和环境因素的影响。各种信号途径通过响应不同的内源信号和环境刺激，形成一个复杂的网络来调控植物叶片的衰老。在本研究中，我们证实两个丝裂原活化蛋白激酶MPK3和MPK6，以及他们上游的MAPK激酶MKK4和MKK5参与调控了植物叶片的衰老。诱导激活功能获得性*MAPKK*突变体*DD*植物能够引起叶片的衰老，但是在功能缺失性的*MAPKK*突变体，*mkk4 mkk5*双突变体中，叶片衰老被延缓。在我们对MAPK信号级联激活后的差异基因表达图谱数据进行分析时，发现拟南芥基质金属蛋白酶基因*MMPs*（*Matrix Metalloproteinases*）的表达被显著上调。基质金属蛋白酶是一种锌钙依赖性的肽链内切酶，广泛存在于动植物中。RT-qPCR分析显示*At-MMP*是一种衰老相关基因，特异在衰老叶片中表达。而且在MAPK被激活后，*At2-MMP*和*At3-MMP*基因的表达均显著上调。同时，我们也发现组成型和诱导过表达*At3-MMP*能够显著促进植物叶片衰老提前。我们的研究证明MKK4/MKK5-MPK3/MPK6-MMPs这条信号级联参与调控拟南芥植物叶片的衰老（Wu et al., *Front Plant Sci*, 2022）。

Regulation of *Arabidopsis* Matrix Metalloproteinases by Mitogen-Activated Protein Kinases and Their Function in Leaf Senescence

Leaf senescence is a developmentally programmed cell death process that is influenced by a variety of endogenous signals and environmental factors. Here, we report that MPK3 and MPK6, two *Arabidopsis* mitogen-activated protein kinases (MAPKs or MPKs), and their two upstream MAPK kinases (MAPKKs or MKKs), MKK4 and MKK5, are key regulators of leaf senescence. Weak induction of constitutively active MAPKKs driven by steroid-inducible promoter, which activates endogenous MPK3 and MPK6, induces leaf senescence. This gain-of-function phenotype requires functional endogenous *MPK3* and *MPK6*. Furthermore, loss of function of both MKK4 and MKK5 delays leaf senescence. Expression profiling leads to the identification of matrix metalloproteinases (*MMPs*), a family of zinc- and calcium-dependent endopeptidases, as the downstream target genes of MPK3/MPK6 cascade. MPK3/MPK6 activation triggered leaf

senescence is associated with rapid and strong induction of *At3-MMP* and *At2-MMP*. Expression of *Arabidopsis* MMP genes is strongly induced during leaf senescence, qualifying them as senescence-associated genes (SAGs). In addition, either constitutive or inducible overexpression of *At3-MMP* is sufficient to trigger leaf senescence. Based on these findings, we conclude that MPK3/MPK6 MAPK cascade and MMP target genes further downstream are involved in regulating leaf senescence in *Arabidopsis* (Wu et al., *Front Plant Sci*, 2022).

（二） 研究成果

发表论文：（*Corresponding author）

Wu H, Si Q, Liu J, Yang L, Zhang S, **Xu J*** (2022) Regulation of *Arabidopsis* matrix metalloproteinases by mitogen-activated protein kinases and their function in leaf senescence. ***Front Plant Sci*** 13: 864986.

（三） 研究队伍

固定人员：

徐娟（课题组长）。

博士后：

邵伊明，张严。

研究生：

司琪，倪敏，刘牛，马宇南，杨腊，苏家豪，钱煜晨，马雅琳。

周　明

课题组

周明，研究员。

研究方向：温度调控植物发育的遗传和表观遗传分子基础。

（一） 研究进展

染色质重塑因子 CLASSY 调控植物组织特异性 DNA 甲基化模式

DNA甲基化（DNA methylation）是一类发生在胞嘧啶5号位碳原子上、可稳定遗传的表观修饰，在动植物基因组中广泛存在。不同组织和细胞内的DNA甲基化模式（DNA methylation patterns）对基因调控、转座沉默及基因印记十分重要，在动植物的许多生物学过程中发挥关键作用。尽管DNA甲基化模式对于这些进程非常重要，然而基因组上每个位点上以及不同组织或细胞内的DNA甲基化模式是如何被调控的，是表观遗传学的一个悬而未决的基本问题。

植物中，从头（de novo）DNA甲基化通过RNA指导的DNA甲基化（RNA-directed DNA methylation, RdDM）途径建立。通过遗传学、表观基因组学和生化分析，我们发现拟南芥中染色质重塑因子CLASSY家族四个成员（*CLSY1-4*）对位点特异性以及全基因组（genome-wide）的DNA甲基化模式的建立至关重要。单个*CLSY*基因调控位点特异性24个核苷酸小干扰RNA（24nt-siRNAs）的产生，这些24nt-siRNAs指导其靶位点DNA甲基化模式的建立。四个*CLSY*一起控制所有RNA聚合酶IV依赖的24nt-siRNAs的产生和从头DNA甲基化模式的建立。ChIPseq数据显示CLSYs调控Pol-IV与染色质关联；生化数据证实，CLSYs依赖于H3K9二甲基化（H3K9me2）和CG类DNA甲基化，调控Pol-IV，建立位点特异性DNA甲基化模式 （Zhou et al., *Nat Genet*, 2018）。

除了对位点特异性DNA甲基化模式的调控，最近我们发现，四个*CLSY*基因在拟南芥中呈现明显的组织表达特异性（Figure 1a, b）。通过遗传和多组学测序分析，我们发现四个*CLSY*是调控拟南芥组织特异性DNA甲基化模式的主要因子。依赖于它们的组织表达特异性，四个*CLSY*基因在全基因组范围内控制组织间特异的DNA甲基化模式；甚至单个*CLSY*就可以改变组织间的DNA甲基化模式（Figure 1c）。总之，我们揭示了*CLSYs*调控植物不同位点和组织间DNA甲基化模式的遗传基础，为利用表观遗传机制改良作物育种提供了可能性。

The CLASSY Family Controls Tissue-Specific DNA Methylation Patterns in *Arabidopsis*

DNA methylation is a stable and heritable epigenetic modification that is essential for gene regulation, transposon silencing and imprinting and plays key roles in both plants and animals.

Although the generation of specific DNA methylation patterns is critical for these processes, how methylation is regulated at individual loci and in different types of tissues and cells remains unclear.

In plants, de novo DNA methylation patterns is established via the pathway termed as RNA-directed DNA methylation (RdDM). With analysis of genetics, epigenome and biochemistry, we covered that the four member CLASSY family (*CLSY1-4*) of chromatin remodeling factors play as master regulators in establishing DNA methylation patterns in *Arabidopsis*. Individually, the *CLSYs* regulate Pol-IV–chromatin association and 24nt-siRNA production at thousands of distinct loci, and together, they regulate essentially all 24nt-siRNAs. Depending on the CLSYs involved, this regulation relies on different repressive chromatin modifications to facilitate locus-specific control of DNA methylation (Zhou et al., *Nat Genet*, 2018).

In addition to their locus-specific roles, recently, we found that these four CLASSY proteins (CLSY1-4), which are differentially expressed during plant development (Figure 1a), play major roles in controlling tissue-specific DNA methylation patterns (Figure 1b). Depending on the tissue, the genetic requirements for specific CLSYs differ significantly and on a global scale, certain *clsy* mutants are sufficient to largely shift the epigenetic landscape between tissues (Figure 1c). Together, these findings not only reveal substantial epigenetic diversity between tissues, but assign these changes to specific CLSY proteins, revealing how locus-specific targeting combined with tissue-specific expression enables the CLSYs to generate epigenetic diversity during plant development.

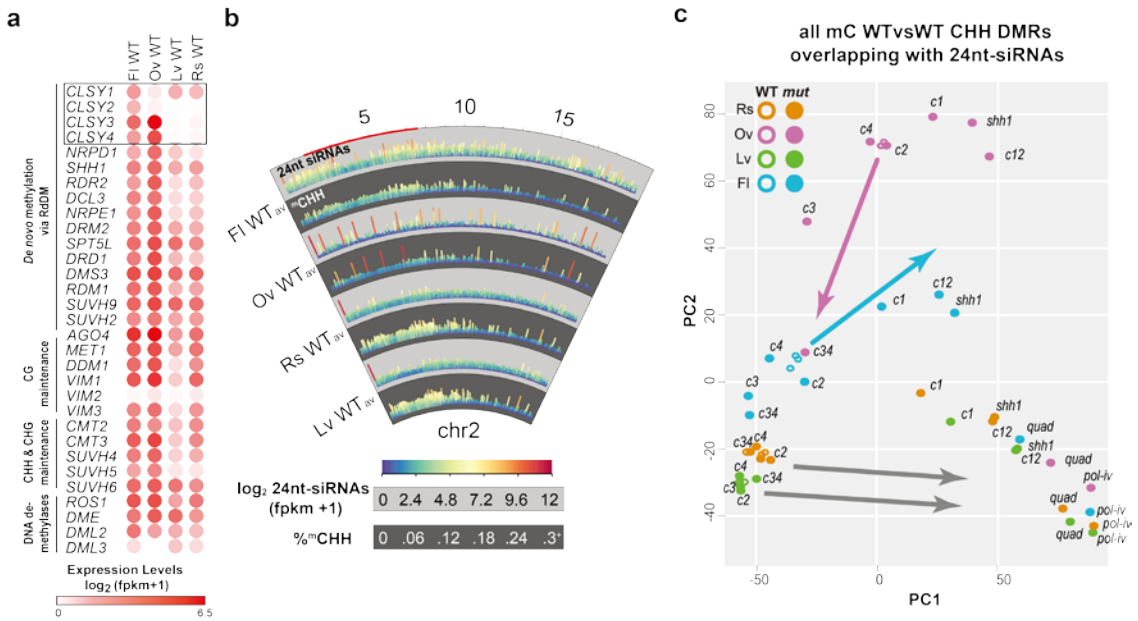


图1、*CLSY*基因家族调控拟南芥组织特异性DNA甲基化模式。（a）*CLSY*家族基因的组织表达特异性。（b）拟南芥花序、心皮、莲座叶和成熟叶片24nt-siRNA和DNA甲基化模式。（c）PCA分析显示*CLSY*家族基因调控拟南芥组织间特异的DNA甲基化模式。

Figure 1. The *CLSY* family controls tissue-specific DNA methylation patterns. (a) The four *CLSY* members show tissues-specific expression patterns. (b) PCA analysis indicated that the *CLSY* family controls tissue-specific DNA

methylation patterns. Fl, flower buds; Ov, ovules; 15 day old rosettes (Rs) (no roots) and 1st and 2nd true leaves (Lv) (from 25 day old plants). The "*c*" indicates *clsy*; *c12* and *c34* represent the double mutants of *clsy1,2* and *clsy3,4*, respectively; and *quad* means the *clsy1,2,3,4*.

（二） 研究成果

发表论文：（*Corresponding author）

1. **Zhou M**, Coruh C, Xu G, Martins L, Bourbousse C, Lambolez A, Law J* (2022) The CLASSY family controls tissue-specific DNA methylation patterns in *Arabidopsis*. ***Nat Commun*** 13:244.
2. 许梦萱，**周明***（2022）植物 RNA 聚合酶 IV 调控 DNA 甲基化和发育的研究进展 **遗传** 44 (7) : 567-580.

（三） 研究队伍

固定人员：

周明（课题组长）。

博士后：

尚菲。

研究生：

许梦萱，王易，张蕊，刘浩林，胡晓舟，张宇涵，陈欣怡，张润佳，陈玥，刘宇庆。

周文焜课题组

周文焜，教授。

研究方向：植物响应胁迫信号的干细胞调控机理。

（一） 研究进展

玉米响应胁迫信号的根干细胞调控机理--玉米遗传材料筛选

实验室围绕植物响应胁迫信号的干细胞调控机理，以须根系玉米为研究对象，挖掘根干细胞响应环境信号的关键调控基因，揭示作物根干细胞的可塑性调控机制。实验室利用中国农业大学玉米平台构建的玉米过表达及CRISPR转基因材料，与亲本ND101比较，初步通过根系长度、侧根数量等筛选玉米主根、侧根表型的转基因株系。目前结果如下：1）筛选获得多份根系表型材料，其中包括转录因子*WRKYa*等主根表型材料5个，*ARRb*等侧根/不定根表型材料3个；2）初步建立了的土培根系实时观察体系；3）建立了玉米根干细胞单细胞测序体系（图 1）。进一步，拟通过在显微镜下观察盐碱胁迫处理后伸长区和分生区的长度、侧根/不定根（冠根）数量等表型，筛选获得玉米根尖分生区、侧根干细胞对盐碱敏感和不敏感的转基因株系，从而挖掘玉米根干细胞响应盐碱胁迫的候选关键调控基因。

Genetic Screening of Primary and Lateral Root Phenotypes in Maize

We excavated key regulatory genes of root stem cells in response to environmental signals in maize. We screened primary and lateral root phenotypes of the maize overexpression and CRISPR transgenic lines constructed by the maize platform of China Agricultural University, and compared them with the parent ND101. The preliminary results are as follows: 1) We identified several primary root phenotypic materials such as transcription factor *WRKYa*, and several lateral/adventitious root phenotypic materials such as *ARRb*; 2) We established real-time rhizotron observation system of soil-based root growth system; 3) A single-cell sequencing system for maize root stem cells (Figure 1). Furthermore, by microscopic observation of the length of the root elongation and meristem region, and the number of lateral roots/adventitious roots after saline-alkali stress treatment, we planned to screen and obtain transgenic strains that are sensitive or insensitive to salt/alkaline in the primary and lateral/adventitious root apical meristem, to explore the candidate key regulatory genes of maize root stem cells in response to salt/alkaline stress.

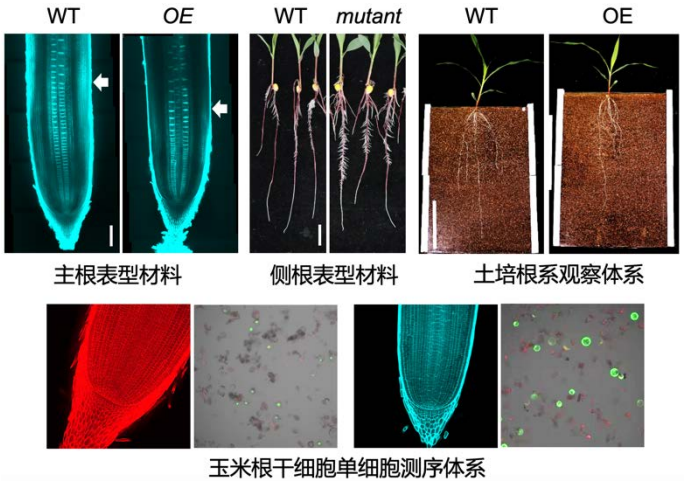


图 1、玉米响应胁迫信号的根干细胞调控机理--玉米遗传材料筛选。

Figure 1. Genetic screening of maize primary and lateral root phenotypes.

（二） 研究成果

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

Zhou W* and Zhang X (2021) Small bending, big curvature. ***J Integr Plant Biol*** 64:3-4.

（三） 研究队伍

固定人员：

周文焜（课题组长）。

研究生：

姜孟丹，赵丽娜，侯雨辰，朱瑞勐，刘瑜，王恬恬，王译爽，邹文丽，乔梓启。

王良省 课题组

王良省，教授。

研究方向：植物光合作用与活性氧信号转导的分子机制。

（一） 研究进展

1、植物叶绿体抗氧化关键因子的筛选与鉴定

叶绿体内单线态氧（$^1O_2$）的过量产生能够通过激活EX1信号转导通路抑制植物生长和诱导细胞死亡。拟南芥*flu/ex1*突变体能够在叶绿体特异的产生$^1O_2$，但是由于$^1O_2$的感受器EX1蛋白缺失而不产生明显的表型。因此，*flu/ex1*可以作为一个研究植物、尤其是叶绿体抵御氧化胁迫的工具，鉴定其中的关键因子。我们对*flu/ex1*进行了再次诱变，通过筛选回复突变体的方法，筛选到了22个对$^1O_2$敏感性恢复的突变体。通过对F2群体进行全基因组测序，寻找候选基因，然后通过遗传互补及突变体重构的方法确定了5个基因。这5个基因编码的蛋白均定位于叶绿体中，具有很高的研究价值。

In the chloroplast of higher plants, overproduction of singlet oxygen ($^1O_2$) activates EX1-meidated signal transduction pathway which leads to growth inhibition of mature plants and cell death of young seedlings. The *Arabidopsis flu/ex1* mutants can produce large amount of $^1O_2$ in the chloroplast but show no obvious phenotype, making it an ideal tool to study the mechanisms by which chloroplast deal with oxidative stress. To find the key components in dealing with oxidative stress of the chloroplast, we mutagenized the *flu/ex1* mutant and screened for the recessive plants that restore their sensitivity to increased amount of $^1O_2$. We isolated a total of 22 mutants and the mutations of these mutants were mapped to 5 genes that were also confirmed by genetic complementation. Proteins encoded by these 5 genes were all localized to the chloroplast, and how these proteins confer chloroplast with increased resistance to oxidative stress needs further exploration.

2、$^1O_2$ 信号通路下游成员的筛选与鉴定

以拟南芥 *flu* 突变体做为专一性产生 $^1O_2$ 的工具，已经发现了两条 $^1O_2$ 信号通路：$^1O_2$-EX1 信号通路和 $^1O_2$-SAFE1 信号通路。为了寻找这两条信号通路的下游组分，我们对 *gEX1-Flag/flu* 和 *flu/ex1/safe1* 种子进行了再一次诱变，从 M2 群体筛选对 $^1O_2$ 不敏感的植株，并鉴定出 12 个基因，且均已经通过遗传互补验证。这些基因编码的蛋白大都定位于叶绿体，但是也有的定位于线粒体、细胞核、细胞质和细胞膜。这表明，$^1O_2$ 介导的细胞死亡和生长抑制需要细胞各个组分的参与。这

12 个基因中至少有 2 个基因既影响 $^1O_2$-EX1 信号通路又影响 $^1O_2$-SAFE1 信号通路，另外 10 个基因可能只影响其中的一条信号转导通路，其参与信号转导的分子机理需要进一步验证。

Taking advantages of the *flu* mutants that can produced large amount of $^1O_2$ in a controlled manner, two $^1O_2$-induced pathways have been identified, the $^1O_2$-EX1 and $^1O_2$-SAFE1 pathway. To find the downstream components of these two pathways, the *gEX1-Flag/flu* and *flu/ex1/safe* seeds were further mutagenized with EMS and screen for seedlings that were insensitive to $^1O_2$ burst. From these two times of mutant screening and mutation mapping, we identified 12 causal genes that were all confirmed by genetic mapping. Among there genes, at least 2 genes are involved in both $^1O_2$-EX1 pathway and $^1O_2$-SAFE1 pathway, the rest 10 genes might function in either of the two pathways. However, the underlying mechanisms by which these genes mediated $^1O_2$ signal need further study.

（三） 研究队伍

固定人员：

王良省（课题组长）。

博士后：

赵欢。

研究生：

赵一凡，张玲玲，孟烨，郭双敏，张璠，胡敏，周德睿，王锋光。

徐　凌

课题组

徐凌，教授。

研究方向：作物与微生物组在逆境下的互作机制。

（一） 研究进展

互作网络揭示微生物组抗逆的复杂性

所有生命活动都离不开水，而全球干旱加剧对许多地方的生产生活造成威胁。在干旱造成的众多严重后果中，农业产量和质量的下降对人类文明的危害最大。植物对干旱胁迫的响应与微生物密切相关。这些微生物一方面受到干旱的胁迫，另一方面微生物也可以影响植物对干旱的耐受性。

然而，关于干旱胁迫下真菌组和细菌组的稳定性是否存在差异这一核心问题，此前仍然缺乏认识。本研究这一问题进行了探究。已知真菌和细菌在生长速率方面存在巨大差异：真菌生长相对较慢，而细菌生长相对更快。据此提出两个假说：1、干旱胁迫下真菌组的抵抗力比细菌组强；2、干旱后复水情景下真菌组的恢复力比细菌组弱。利用之前已发表真菌组和细菌组数据，分别在群落组成层面和物种关联层面对这两个假说进行检验。

在群落组成层面上，发现与细菌组相比，真菌组对干旱胁迫的抵抗力更强，且在复水后真菌组的恢复力较弱。奇怪的是真菌组的恢复力在复水第一周比细菌组更强，在物种关联层面上的结果更复杂，总体上干旱破坏了细菌-细菌之间，真菌-真菌之间以及细菌-真菌之间的共现网络。令人惊讶的是，根际真菌和叶际细菌的功能类群间的共现网络因干旱而得到加强，在根际中涉及丛枝菌根真菌的共现网络也是如此。利用该数据对胁迫梯度假说进行了检验。该假说认为，在干旱等胁迫情景下，物种间的竞争减弱，而正相互作用频率增加。发现干旱增加了正相关关系的相对频率，支持胁迫梯度假说。并且还从共现网络中检测到了很多枢纽（Gao et al., *Nat Commun*, 2022）。

Co-occurrence Networks Reveal More Complexity Than Community Composition in Resistance and Resilience of Microbial Communities

Plant response to drought stress involves fungi and bacteria that live on and in plants and in the rhizosphere, yet the stability of these myco- and micro-biomes remains poorly understood. We investigate the resistance and resilience of fungi and bacteria to drought in an agricultural system using both community composition and microbial associations. Here we show that tests of the fundamental hypotheses that fungi, as compared to bacteria, are (i) more resistant to drought

stress but (ii) less resilient when rewetting relieves the stress, found robust support at the level of community composition. Results were more complex using all-correlations and co-occurrence networks. In general, drought disrupts microbial networks based on significant positive correlations among bacteria, among fungi, and between bacteria and fungi. Surprisingly, co-occurrence networks among functional guilds of rhizosphere fungi and leaf bacteria were strengthened by drought, and the same was seen for networks involving arbuscular mycorrhizal fungi in the rhizosphere. We also found support for the stress gradient hypothesis because drought increased the relative frequency of positive correlations (Gao et al., *Nat Commun*, 2022).

（二） 研究成果

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

Gao, C#*, **Xu, L#**, Montoya, L, Madera, M, Hollingsworth, J, Chen, L, Purdom, E, Singan, V, Vogel, J, Hut (一) macher, R B, Dahlberg, J A, Coleman-Derr, D, Lemaux, P G, **Taylor, J W*** (2022) Co-occurrence networks reveal more complexity than community composition in resistance and resilience of microbial communities ***Nat Commun*** 13: 3867.

（三） 研究队伍

固定人员：

徐凌（课题组长）。

研究生：

王惠茹，陶艺元，崔雪屹，白玉芳，张瑞，苏明，孙倩。

附录、重要科研论文首页

（影响因子 9 以上论文首页 38 篇）

植物生理学与生物化学国家重点实验室

State Key Laboratory of Plant Physiology and Biochemistry

http://sklppb.cau.edu.cn/

附录

RESEARCH ARTICLE SUMMARY

CROP GENOMICS

Convergent selection of a WD40 protein that enhances grain yield in maize and rice

Wenkang Chen†, Lu Chen†, Xuan Zhang†, Ning Yang†, Jianghua Guo, Min Wang, Shenghui Ji, Xiangyu Zhao, Pengfei Yin, Lichun Cai, Jing Xu, Lili Zhang, Yingjia Han, Yingni Xiao, Gen Xu, Yuebin Wang, Shuhui Wang, Sheng Wu, Fang Yang, David Jackson, Jinkui Cheng, Saihua Chen, Chuanqing Sun, Feng Qin, Feng Tian, Alisdair R. Fernie, Jiansheng Li*, Jianbing Yan*, Xiaohong Yang*

INTRODUCTION: During the independent process of cereal evolution, many trait shifts appear to have been under convergent selection to meet the specific needs of humans. Identification of convergently selected genes across cereals could help to clarify the evolution of crop species and to accelerate breeding programs. In the past several decades, researchers have debated whether convergent phenotypic selection in distinct lineages is driven by conserved molecular changes or by diverse molecular pathways. Two of the most economically important crops, maize and rice, display some conserved phenotypic shifts—including loss of seed dispersal, decreased seed dormancy, and increased grain number during evolution—even though they experienced independent selection. Hence, maize and rice can serve as an excellent system for understanding the extent of convergent selection among cereals.

RATIONALE: Despite the identification of a few convergently selected genes, our understanding of the extent of molecular convergence on a genome-wide scale between maize and rice is very limited. To learn how often selection acts on orthologous genes, we investigated the functions and molecular evolution of the grain yield quantitative trait locus *KRN2* in maize and its rice ortholog *OsKRN2*. We also identified convergently selected genes on a genome-wide scale in maize and rice, using two large datasets.

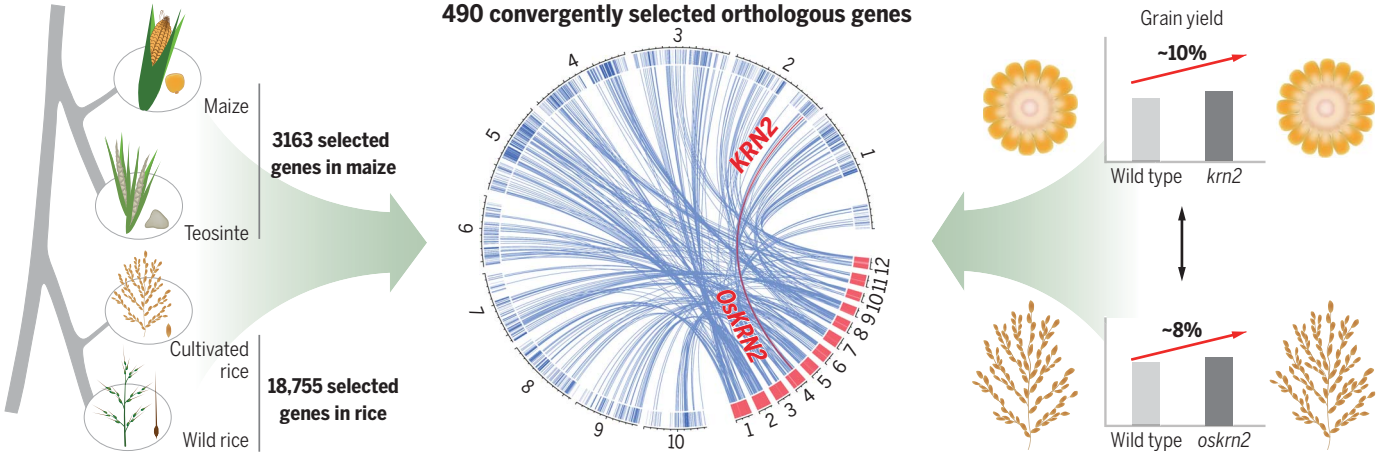
RESULTS: We identified a selected gene, *KRN2* (*kernel row number2*), that differs between domesticated maize and its wild ancestor, teosinte. This gene underlies a major quantitative trait locus for kernel row number in maize. Selection in the noncoding upstream regions resulted in a reduction of *KRN2* expression and an increased grain number through an increase in kernel rows. The rice ortholog, *OsKRN2*, also underwent selection and negatively regulates grain number via control of secondary panicle branches. These orthologs encode WD40 proteins and function synergistically with a gene of unknown function, DUF1644, which suggests that a conserved protein interaction controls grain number in maize and rice. Field tests show that knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by ~10% and ~8%, respectively, with no apparent trade-off in other agronomic traits. This suggests potential applications of *KRN2* and its orthologs for crop improvement.

On a genome-wide scale, we identified a set of 490 orthologous genes that underwent convergent selection during maize and rice evolution, including *KRN2/OsKRN2*. We found that the convergently selected orthologous genes appear to be significantly enriched in two specific pathways in both maize and rice: starch and sucrose metabolism, and biosynthesis of cofactors. A deep analysis of convergently selected genes in the starch metabolic pathway indicates that the degree of genetic convergence via convergent selection is related to the conservation and complexity of the gene network for a given selection.

CONCLUSION: Our findings show that common phenotypic shifts during maize and rice evolution acting on conserved genes are driven at least in part by convergent selection, which in maize and rice likely occurred both during and after domestication. We provide evolutionary and functional evidence on the convergent selection of *KRN2/OsKRN2* for grain number between maize and rice. We further found that a complete loss-of-function allele of *KRN2/OsKRN2* increased grain yield without an apparent negative impact on other agronomic traits. Exploring the role of *KRN2/OsKRN2* and other convergently selected genes across the cereals could provide new opportunities to enhance the production of other global crops. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: yxiaohong@cau.edu.cn (X.Y.); yjianbing@mail.hzau.edu.cn (J.Y.); lijiansheng@cau.edu.cn (J.L.)
†These authors contributed equally to this work.
Cite this article as W. Chen *et al.*, *Science* **375**, eabg7985 (2022). DOI: 10.1126/science.abg7985

READ THE FULL ARTICLE AT
https://doi.org/10.1126/science.abg7985



Shared selected orthologous genes in maize and rice for convergent phenotypic shifts during domestication and improvement. By comparing 3163 selected genes in maize and 18,755 selected genes in rice, we identified 490 orthologous gene pairs, including *KRN2* and its rice ortholog *OsKRN2*, as having been convergently selected. Knockout of *KRN2* in maize or *OsKRN2* in rice increased grain yield by increasing kernel rows and secondary panicle branches, respectively.

附录

Trends in Biotechnology

CellPress

Forum

Dissecting the plant chromatin interactome using mass spectrometry

Yanmei Chen,[1,4,*] Jun Xiao,[2] and Peng Liu[3,4]

The protein interactome mediates crucial functions in transcription, chromatin remodeling, and higher-order structural organization. Elucidating the proteins that interact with chromatin-associated RNA or proteins is key to understanding fundamental epigenetic regulatory pathways. We discuss the opportunities and challenges of mass spectrometry (MS)-based proteomics for characterizing the plant chromatin interactome.

Chromatin is a macromolecular complex of DNA and histone proteins arranged into nucleosomes which are present in almost every eukaryotic cell. As the basic functional unit of chromatin, the nucleosome in eukaryote cells is composed of four core histone octamers (H3, H4, H2A, and H2B) wrapped with 147 bp of DNA. Chromatin structure affects gene expression and is tightly regulated by DNA methylation, histone post-translational modifications (PTMs), and by interactions between proteins and chromatin [1] (Figure 1) [1]. Epigenetic mechanisms including covalent histone PTMs, chromatin accessibility, and chromatin-associated protein interaction networks create various chromatin states for stress-responsive gene expression, which is important for plant adaptation to external environmental stimuli (Figure 1). Establishing how these proteins interact with chromatin would provide clues to their function in the global epigenetic regulation of genomes. Key to this endeavor is to

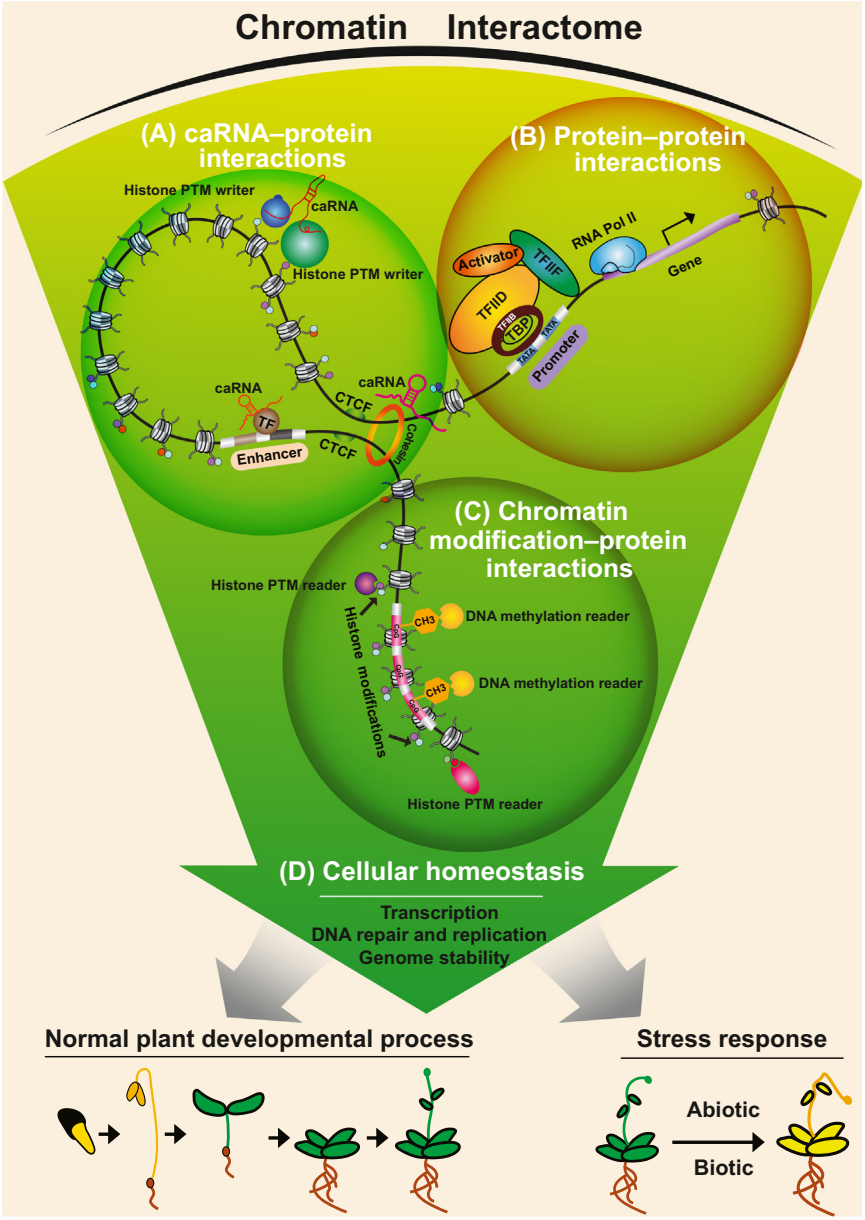


Figure 1. The diverse landscape of the chromatin-associated interactome in plants. (A) Interactions between chromatin-associated RNA and proteins. Chromatin-associated RNA (caRNA) is a newly identified class of RNA molecules that are stably linked to chromatin, where they establish the chromatin status of genes by interacting with various RNA-binding proteins. caRNA can also modulate the recruitment of transcription factors (TFs), chromatin modifiers (e.g., histone modification writers), and chromatin remodelers (e.g., CTCF and cohesin) bound to chromatin. The resulting caRNA–protein complexes serve as coregulators for chromatin remodeling, transcriptional activation, and gene expression. (B) Interactions between chromatin-associated protein complexes. In plants, various types of proteins including TFs, RNA polymerase-associated proteins, histone-binding regulators, and chromatin regulators are recruited to chromatin; these are defined as chromatin-associated proteins. Protein interactions among chromatin-associated protein complexes modulate gene assembly at the promoter, further initiating downstream transcriptional programs as well as

(Figure legend continued at the bottom of the next page.)

附录

Trends in
Biochemical Sciences

CellPress

Forum

Mapping histone modification-dependent protein interactions with chemical proteomics

Yanmei Chen[1,*] and Yi Wang[2]

Post-translational modifications (PTMs) of histones play essential roles in chromatin function and epigenetic regulation. Determining the interaction partners of these modifications is crucial to understanding transcriptional processes related to diverse developmental and pathological cues. We discuss how chemical proteomics can be applied to the simultaneous and global exploration of these interaction networks.

Chromatin biology and histone modifications

In eukaryotic cells, an octameric histone complex composed of two copies of each of the four core histone proteins (H3, H4, H2A, and H2B) interacts with DNA through electrostatic interactions and compacts into nucleosomes, which function as the basic unit of chromatin. A key feature of nucleosomes is their plethora of histone post-translational modifications (hPTMs), which are deposited at N-terminal tails of histones and are highly regulated to control chromatin dynamics and transcriptional programs (Figure 1). hPTMs regulate chromatin structure, folding, and function, by recruiting hPTM-readers and their associated binding partners (effector proteins) or by inhibiting the binding of proteins to chromatin (Figure 1) [1]. Dysregulation of these processes is linked to a range of human disorders; indeed, therapies targeting hPTM–protein interactions have entered clinical trials for cancer treatment, and several modifying and de-modifying enzymes have been used as promising targets for new anticancer drugs [2]. Understanding these regulatory pathways at the molecular level not only illuminates fundamental biology, but also reveals how perturbation of these interactions can lead to disease. However, characterizing how this chemical language embedded in chromatin defines the protein interactome of the genome remains a major challenge.

Common methods to determine the interactions of hPTMs are often applied at the peptide level, using synthetic histone peptides, or by enrichment through chromatin immunoprecipitation assays (ChIP). Although such studies have enhanced our knowledge of the interactions between proteins and hPTMs, these methods are limited by antibody cross-reactivity or require access to the underlying DNA, both of which can lead to false negatives or chromatin disruption. Novel approaches that are enhancing our understanding of hPTM-triggered interactions include the generation of analogous full-length 'protein probes' with an hPTM at a desired site and also labeled with an affinity probe. With the ongoing improvements in high-resolution mass spectrometry (MS) and data processing, chemical proteomics has emerged as a powerful approach to elucidate the underlying processes of hPTM-binding protein complexes around chromatin. Here, we provide an overview of three chemical proteomic approaches in mapping protein interaction networks associated with hPTMs.

Characterizing hPTM-associated protein interactions

Compared with traditional biochemical methods, chemical proteomics offers the advantage of systematic and unbiased mapping of hPTM readers and their binding proteins. These methods rely on specific chemical probes that can covalently capture hPTM-mediated protein interactors of interest from living cells, which then can be identified by quantitative MS. Much progress has been made in using various chemical proteomic approaches to characterize hPTM-associated protein interactions. These methods can be classed into photo-crosslinking and proximity biotinylation strategies.

Photo-crosslinking

To circumvent the low sensitivity and specificity of ChIP-sequencing, photoaffinity groups can be incorporated into bait proteins to convert noncovalent interactions to irreversible chemical linkages by photo-crosslinking [3]. Using genetically coded probes or synthetic peptides, these approaches are capable of capturing endogenous hPTM-interacting partners at the single-protein level or from complex samples [4]. However, large-scale analysis of hPTM-interacting partners remains challenging because of limitations in the enrichment and analysis of crosslinked peptides.

To tackle these difficulties, traditional photoaffinity groups in synthetic hPTM-containing peptide probes were modified by introducing a cleavable disulfide moiety into a tri-functional noncanonical amino acid alkynyl diazirino disulfanyl cysteine (ADdis–Cys) [5]. After cleavage, the photo-crosslinked interactors can be easily released from the probes, maintaining an MS-stable tag amenable to 'click' chemistry modification enrichment and MS analysis (Figure 2A) [5]. ADdis–Cys-MS is efficient in capturing many low-abundance or low-affinity interacting proteins (e.g., hPTM–reader interaction surface. This approach can be used for simultaneous detection and mapping of hPTM-interacting readers in complex proteomes. Although the ADdis–Cys moiety may prevent the hPTM–reader interaction, this can be circumvented by using several histone peptides with different distances between the hPTM and ADdis–Cys site. Due to the broad applicability of these probes, ADdis–Cys-MS can be also extended for detecting and mapping protein interactors of non-histone PTMs. However, this

附录

CellPress
Partner Journal

Molecular Plant
Research Article

RAF22, ABI1 and OST1 form a dynamic interactive network that optimizes plant growth and responses to drought stress in *Arabidopsis*

Zhihui Sun[1], Zhenkai Feng[1], Yanglin Ding[1], Yuanpeng Qi[1], Shan Jiang[1], Zhen Li[1], Yu Wang[1], Junsheng Qi[1], Chunpeng Song[2], Shuhua Yang[1] and Zhizhong Gong[1,3,*]

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China

[2]Collaborative Innovation Center of Crop Stress Biology, Institute of Plant Stress Biology, Henan University, Kaifeng 475001, China

[3]School of Life Sciences, Institute of Life Science and Green Development, Hebei University, Baoding 100193, China

***Correspondence: Zhizhong Gong (gongzz@cau.edu.cn)**

https://doi.org/10.1016/j.molp.2022.06.001

ABSTRACT

Plants adapt to their ever-changing environment via positive and negative signals induced by environmental stimuli. Drought stress, for instance, induces accumulation of the plant hormone abscisic acid (ABA), triggering ABA signal transduction. However, the molecular mechanisms for switching between plant growth promotion and stress response remain poorly understood. Here we report that RAF (rapidly accelerated fibrosarcoma)-LIKE MITOGEN-ACTIVATED PROTEIN KINASE KINASE KINASE 22 (RAF22) in *Arabidopsis thaliana* physically interacts with ABA INSENSITIVE 1 (ABI1) and phosphorylates ABI1 at Ser416 residue to enhance its phosphatase activity. Interestingly, ABI1 can also enhance the activity of RAF22 through dephosphorylation, reciprocally inhibiting ABA signaling and promoting the maintenance of plant growth under normal conditions. Under drought stress, however, the ABA-activated OPEN STOMATA1 (OST1) phosphorylates the Ser81 residue of RAF22 and inhibits its kinase activity, restraining its enhancement of ABI1 activity. Taken together, our study reveals that RAF22, ABI1, and OST1 form a dynamic regulatory network that plays crucial roles in optimizing plant growth and environmental adaptation under drought stress.

Key words: ABA signaling, RAF22, ABI1, OST1, phosphorylation

Sun Z., Feng Z., Ding Y., Qi Y., Jiang S., Li Z., Wang Y., Qi J., Song C., Yang S., and Gong Z. (2022). RAF22, ABI1 and OST1 form a dynamic interactive network that optimizes plant growth and responses to drought stress in *Arabidopsis*. Mol. Plant. **15**, 1192–1210.

INTRODUCTION

Global warming is predicted to cause environmental changes that will threaten plant survival and crop yields worldwide (Chen et al., 2021b; Zhang et al., 2022). Understanding the molecular mechanisms plants use to respond to these changes is paramount for breeding crops that resist these stresses and stabilizing production (Chen et al., 2021b; Zhang et al., 2022). In response to environmental stresses such as drought, plants rapidly accumulate abscisic acid (ABA), which binds the PYRABACTIN RESISTANCE 1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR) ABA receptors. These receptors, in turn, bind to and inhibit the activity of clade A protein phosphatase 2Cs (PP2Cs). Formation of this complex leads to activation of protein kinases such as SNF1-related protein kinase 2s (SnRK2s) and the plasma membrane receptor-like protein kinase GUARD CELL HYDROGEN PEROXIDE-RESISTANT 1 (GHR1), which are inhibited by PP2Cs in the absence of ABA (Cutler et al., 2010; Hua et al., 2012; Zhu, 2016; Chen et al., 2020, 2021b; Zhang et al., 2022). The activated SnRK2s phosphorylate downstream targets such as SLOW ANION CHANNEL-ASSOCIATED 1 (SLAC1) and the R-type anion channel QUAC1 while inactivating the K^+ inward-rectifying channel (KAT1) to promote stomatal closure and reduce evapotranspiration and photosynthesis. SnRK2s also activate ABRE-BINDING proteins (AREBs)/ABRE-BINDING FACTOR (ABF) transcription factors, which regulate the expression of stress response genes to reprogram metabolism, induce osmolyte accumulation, slow plant growth, or promote senescence (Geiger et al., 2009, 2010; Meyer et al., 2010; Imes et al.,

Published by the Molecular Plant Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

附录

CellPress
Partner Journal

Molecular Plant
Research Article

Arabidopsis SYP121 acts as an ROP2 effector in the regulation of root hair tip growth

Xiankui Cui[1,4], Shuwei Wang[1,4], Yaohui Huang[1], Xuening Ding[1], Zirong Wang[1], Lidan Zheng[1], Yujing Bi[1], Fanghui Ge[1], Lei Zhu[1,2], Ming Yuan[1], Shaul Yalovsky[3] and Ying Fu[1,2,*]

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China

[2]Joint Laboratory for International Cooperation in Crop Molecular Breeding, Ministry of Education, China Agricultural University, Beijing 100193, China

[3]Department of Plant Sciences, Tel Aviv University, Tel Aviv 69978, Israel

[4]These authors contributed equally to this article.

***Correspondence: Ying Fu (yingfu@cau.edu.cn)**

https://doi.org/10.1016/j.molp.2022.04.008

ABSTRACT

Tip growth is an extreme form of polarized cell expansion that occurs in all eukaryotic kingdoms to generate highly elongated tubular cells with specialized functions, including fungal hyphae, animal neurons, plant pollen tubes, and root hairs (RHs). RHs are tubular structures that protrude from the root epidermis to facilitate water and nutrient uptake, microbial interactions, and plant anchorage. RH tip growth requires polarized vesicle targeting and active exocytosis at apical growth sites. However, how apical exocytosis is spatially and temporally controlled during tip growth remains elusive. Here, we report that the Qa-Soluble *N*-ethylmaleimide-sensitive factor attachment protein receptor (SNARE) SYP121 acts as an effector of Rho of Plants 2 (ROP2), mediating the regulation of RH tip growth. We show that active ROP2 promotes SYP121 targeting to the apical plasma membrane. Moreover, ROP2 directly interacts with SYP121 and promotes the interaction between SYP121 and the R-SNARE VAMP722 to form a SNARE complex, probably by facilitating the release of the Sec1/Munc18 protein SEC11, which suppresses the function of SYP121. Thus, the ROP2-SYP121 pathway facilitates exocytic trafficking during RH tip growth. Our study uncovers a direct link between an ROP GTPase and vesicular trafficking and a new mechanism for the control of apical exocytosis, whereby ROP GTPase signaling spatially regulates SNARE complex assembly and the polar distribution of a Q-SNARE.

Key words: ROP GTPase, SYP121, SNARE protein, exocytosis, root hair, tip growth

Cui X., Wang S., Huang Y., Ding X., Wang Z., Zheng L., Bi Y., Ge F., Zhu L., Yuan M., Yalovsky S., and Fu Y. (2022). *Arabidopsis* SYP121 acts as an ROP2 effector in the regulation of root hair tip growth. Mol. Plant. **15**, 1008–1023.

INTRODUCTION

Plant cell polar growth gives rise to cells with specific shapes that are associated with specialized functions, and it is therefore intimately related to plant growth and development. Root hairs (RHs) are protrusions of trichoblast cells in the root epidermis that adopt an extreme form of polar growth known as tip growth. These structures play important roles in water and nutrient uptake, microbial interactions, and plant anchorage. Moreover, RHs also serve as an ideal model system for studying polar cell growth and plant responses to the environment (Foreman and Dolan, 2001; Cole and Fowler, 2006; Libault et al., 2010).

RH initiation and tip growth require the polar delivery of components of the plasma membrane (PM) and cell walls to a specialized growth site (Gu and Nielsen, 2013). Therefore, controlling vesicle-mediated polarized exocytosis in secretory pathways is critical for RH formation. Several Rho of Plants (ROPs), e.g., ROP2, 4, and 6, have been shown to control RH tip growth by orchestrating pH, Ca^{2+}, and reactive oxygen species signaling (Molendijk et al., 2001; Jones et al., 2002, 2007; Bloch et al., 2005, 2011; Carol et al., 2005; Duan et al., 2010; Sorek et al., 2010; Denninger et al., 2019). Moreover, some ROP effectors have been implicated in the regulation of vesicle trafficking in different cell types, either through regulating Ca^{2+} and F-actin dynamics (e.g., RIC1, 3, and 4) or potentially interacting with the exocyst vesicle-tethering complex subunit SEC3 (e.g., ICR1) (Gu et al., 2005; Lavy et al., 2007; Lee et al., 2008; Fu, 2010; Lin et al., 2012; Nagawa et al., 2012; Zhou et al., 2015). Genetic analyses also suggest that the trans-Golgi network-localized

Published by the Molecular Plant Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

附录

CellPress
Partner Journal

Molecular Plant
Research Article

Natural variations of *ZmSRO1d* modulate the trade-off between drought resistance and yield by affecting ZmRBOHC-mediated stomatal ROS production in maize

Huajian Gao[1,2,3], Junjun Cui[3], Shengxue Liu[3,4], Shuhui Wang[3], Yongyan Lian[3], Yunting Bai[3], Tengfei Zhu[3], Haohao Wu[3], Yijie Wang[3], Shiping Yang[3], Xuefeng Li[3], Junhong Zhuang[3,4], Limei Chen[3,4], Zhizhong Gong[3,4,5] and Feng Qin[3,4,*]

[1]Key Laboratory of Plant Molecular Physiology, Institute of Botany, Chinese Academy of Sciences; Beijing 100093, China

[2]University of Chinese Academy of Sciences; Beijing 100049, China

[3]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University; Beijing 100193, China

[4]Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University; Beijing 100193, China

[5]School of Life Science, Institute of Life Science and Green Development, Hebei University, Baoding, Hebei, 071002, China

***Correspondence: Feng Qin (qinfeng@cau.edu.cn)**

https://doi.org/10.1016/j.molp.2022.08.009

ABSTRACT

While crop yields have historically increased, drought resistance has become a major concern in the context of global climate change. The trade-off between crop yield and drought resistance is a common phenomenon; however, the underlying molecular modulators remain undetermined. Through genome-wide association study, we revealed that three non-synonymous variants in a drought-resistant allele of *ZmSRO1d-R* resulted in plasma membrane localization and enhanced mono-ADP-ribosyltransferase activity of ZmSRO1d toward ZmRBOHC, which increased reactive oxygen species (ROS) levels in guard cells and promoted stomatal closure. *ZmSRO1d-R* enhanced plant drought resilience and protected grain yields under drought conditions, but it led to yield drag under favorable conditions. In contrast, loss-of-function mutants of *ZmRBOHC* showed remarkably increased yields under well-watered conditions, whereas they showed compromised drought resistance. Interestingly, by analyzing 189 teosinte accessions, we found that the *ZmSRO1d-R* allele was present in teosinte but was selected against during maize domestication and modern breeding. Collectively, our work suggests that the allele frequency reduction of *ZmSRO1d-R* in breeding programs may have compromised maize drought resistance while increased yields. Therefore, introduction of the *ZmSRO1d-R* allele into modern maize cultivars would contribute to food security under drought stress caused by global climate change.

Key words: ZmSRO1d, stomatal ROS, drought resistance, yield, maize

Gao H., Cui J., Liu S., Wang S., Lian Y., Bai Y., Zhu T., Wu H., Wang Y., Yang S., Li X., Zhuang J., Chen L., Gong Z., and Qin F. (2022). Natural variations of *ZmSRO1d* modulate the trade-off between drought resistance and yield by affecting ZmRBOHC-mediated stomatal ROS production in maize. Mol. Plant. **15**, 1558–1574.

INTRODUCTION

Maize is a major cereal crop worldwide; however, the yields are frequently limited by drought, a major environmental stress that has increased globally due to climate change and erratic rainfall patterns (Gupta et al., 2020). Thus, a central goal of current breeding programs is to reduce the drought sensitivity of yield to ensure a sustainable food supply for the increasing global population. Although yield potential has historically increased in many agricultural regions owing to modern breeding efforts, yield sensitivity to limited soil water availability has been reported to have increased (Lobell et al., 2014, 2020). The trade-off between crop yields and drought resistance is a

Published by the Molecular Plant Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

CellPress
Partner Journal

Molecular Plant
Correspondence

Optimized prime editing efficiently generates glyphosate-resistant rice plants carrying homozygous TAP-IVS mutation in *EPSPS*

Yun Zhou[2,3], Xue-Chen Wang[1] and Qi-Jun Chen[1,4,]*

Dear Editor,

Prime editing is a novel and universal CRISPR-Cas-derived precise genome-editing technology and has great potentials for applications in basic plant research and crop molecular breeding (Anzalone et al., 2019). Although low efficiency has restrained the original prime editors (PEs) from being used as a routine tool for precise genome editing in plants, an iterative update of the PEs is removing this obstacle (Lin et al., 2021; Xu et al., 2022). Recently, the Liu group reported three optimization strategies for improving prime editing efficiency (Chen et al., 2021; Nelson et al., 2022). The first strategy is based on engineered prime editing guide RNAs (epegRNAs), which were generated by incorporating structured RNA motifs to the 3′ terminus of pegRNAs. This strategy enhances pegRNA stability and prevents degradation of the 3′ extension (Nelson et al., 2022). The second strategy is based on the optimized PE2 protein (PEmax), which harbors a SpCas9 variant with increased nuclease activity, an additional nuclear localization signal (NLS) sequences, and a new linker between nCas9 and reverse transcriptase (Chen et al., 2021). The third strategy is based on inhibition of DNA mismatch repair (MMR) in cells (Chen et al., 2021). In this work, we tested the optimized PEs generated with these three strategies in rice, demonstrating that the optimized PEs greatly improved prime editing efficiency in rice. We named the two optimized PEs ePE3max and ePE5max: the former is comprised of the PEmax protein, an epegRNA with evopreQ1 appended to its 3′ end, and a nicking sgRNA; the latter is comprised of the ePE3max system and a dominant negative OsMLH1 variant for inhibiting MMR. Using the two optimized PEs, we efficiently generated homozygous and heterozygous T173I, A174V, and P177S (TAP-IVS) mutation in *EPSPS* in rice, which lays a solid foundation for rice non-transgenic glyphosate-resistance breeding.

TAP-IVS mutation (T102I, A103V, and P106S) is a naturally occurring EPSPS triple substitution found in the highly glyphosate resistant *Amaranthus hybridus* population from Argentina (Perotti et al., 2019). Less or little fitness cost associated with the homozygous TAP-IVS mutation accounted for the proliferation of the mutants within the population, even in absence of glyphosate (Perotti et al., 2019). Since non-transgenic glyphosate-resistance rice varieties have great values in agriculture, we wondered whether we were able to use the optimized PEs to efficiently generate the TAP-IVS mutation in *OsEPSPS* for rice non-transgenic glyphosate-resistance breeding (Perotti et al., 2019; Li et al., 2020). Thus, we tested the optimized PEs for installation of the TAP-IVS edits in *EPSPS* in rice protoplasts. Our results indicate that the PEmax architecture improved prime editing efficiency and could synergize with the epegRNA (pegRNA-evopreQ1) in rice protoplasts (Figure 1A).

Since the ePE3max, which is comprised of the PEmax protein, an epegRNA, and a nicking sgRNA, achieved the highest editing efficiency (Figure 1A), we then asked whether we were able to further improve editing efficiency of the ePE3max by co-expressing dominant negative OsMLH1 variants. We generated codon-optimized OsMLH1dn, OsMLH1 E44A, OsMLH1dn E44A, and OsMLH1 1-393-2xNLS, corresponding to human MLH1dn, MLH1 E34A, MLH1dn E34A, and MLH1 1-335-NLS, respectively (Chen et al., 2021). These variants could integrate into the MMR complex in replacement of OsMLH1 with normal function and interfere the function of MMR, leading to inhibition of MMR. These OsMLH1 variants and the ePE3max constitute the ePE5max system. The ePE5max system did not further improve editing efficiency of the ePE3max in rice protoplasts (Figure 1A).

To generate rice lines harboring the TAP-IVS mutation, we generated two optimized PEs, ePE3max-TAP and ePE5max-TAP, for rice transformation (Figure 1B). We also generated two control PEs, PE3-TAP and PE5-TAP, which harbor the original PE protein and pegRNA, for comparison with the two optimized PEs in rice transgenic lines. We transformed rice with these four PEs. We analyzed the edits by the Sanger sequencing of PCR fragments amplified from the transgenic lines (Figure 1C) and next-generation sequencing of PCR amplicons. Next-generation sequencing results indicate that the ePE3max and ePE5max significantly improved editing efficiency in rice transgenic lines compared with PE3 and PE5, respectively (Figure 1D). The ePE5max had similar efficiency of heritable mutations (homozygous and heterozygous) to the ePE3max but had higher efficiency of homozygous mutations than the ePE3max. Using the ePE5max, we achieved 6.1% (10/163) homozygous TAP-IVS mutant lines (Figure 1D; Supplemental Table 1).

We transplanted the homozygous TAP-IVS mutant lines and transgenic lines without edits (control) to soil and sprayed 10 mM glyphosate on the seedlings. As expected, the mutant plants showed reliable tolerance compared with the control (Figure 1E). As we previously reported (Jiang et al., 2020), in this study, once again we observed the new type of byproducts in rice protoplasts and transgenic lines (Figure 1A; Supplemental Figure 1). This type of undesired edits, which we

Published by the Molecular Plant Shanghai Editorial Office in association with Cell Press, an imprint of Elsevier Inc., on behalf of CSPB and CEMPS, CAS.

nature plants

Article

https://doi.org/10.1038/s41477-022-01254-3

Natural polymorphism of ZmICE1 contributes to amino acid metabolism that impacts cold tolerance in maize

Received: 7 March 2021

Accepted: 8 September 2022

Published online: 14 October 2022

Check for updates

Haifang Jiang[1,5], Yiting Shi[1,5], Jingyan Liu[1,2,5], Zhen Li[1,5], Diyi Fu[1], Shifeng Wu[1], Minze Li[1], Zijia Yang[1], Yunlu Shi[1], Jinsheng Lai[1,3], Xiaohong Yang[1,3], Zhizhong Gong[1], Jian Hua[4] and Shuhua Yang[1]

Cold stress negatively affects maize (*Zea mays* L.) growth, development and yield. Metabolic adjustments contribute to the adaptation of maize under cold stress. We show here that the transcription factor INDUCER OF CBF EXPRESSION 1 (ZmICE1) plays a prominent role in reprogramming amino acid metabolome and *COLD-RESPONSIVE* (*COR*) genes during cold stress in maize. Derivatives of amino acids glutamate/asparagine (Glu/Asn) induce a burst of mitochondrial reactive oxygen species, which suppress the cold-mediated induction of *DEHYDRATION RESPONSE ELEMENT-BINDING PROTEIN 1* (*ZmDREB1*) genes and impair cold tolerance. ZmICE1 blocks this negative regulation of cold tolerance by directly repressing the expression of the key Glu/Asn biosynthesis genes, *ASPARAGINE SYNTHETASEs*. Moreover, ZmICE1 directly regulates the expression of *DREB1s*. Natural variation at the *ZmICE1* promoter determines the binding affinity of the transcriptional activator ZmMYB39, a positive regulator of cold tolerance in maize, resulting in different degrees of *ZmICE1* transcription and cold tolerance across inbred lines. This study thus unravels a mechanism of cold tolerance in maize and provides potential targets for engineering cold-tolerant varieties.

Cold stress is a major environmental stress that threatens agricultural production and restricts the distribution of many important crops. Plants have developed various physiological, molecular and metabolic responses that allow them to withstand cold stress. In *Arabidopsis thaliana* and rice (*Oryza sativa*), some key regulators for sensing and transducing cold signals have been identified[1–4], including the regulatory cascade of transcription factors DEHYDRATION RESPONSE ELEMENT-BINDING PROTEIN 1 (DREB1)[5–7]. The DREB1 family activates the expression of a large number of *COLD-RESPONSIVE* (*COR*) genes to promote cold tolerance[7,8]. *DREB1* genes are directly regulated by INDUCER OF CBF EXPRESSION 1 (ICE1), a MYC-like basic helix-loop-helix transcriptional activator[9,10]. The ICE1-DREB1-COR cascade is regulated by protein kinases that are activated by cold stress to modulate cold tolerance[11–15].

Maize (*Zea mays* L.) is one of the most widely cultivated crops worldwide. It originated from tropical areas and is susceptible to cold stress during seed germination and seedling growth especially in early spring[16–18]. Thus, improving cold tolerance in maize during early growth

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing, China. [2]Fresh Corn Research Center of BTH, Tianjin Agricultural University, Tianjin, China. [3]National Maize Improvement Center, Department of Plant Genetics and Breeding, China Agricultural University, Beijing, China. [4]Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY, USA. [5]These authors contributed equally: Haifang Jiang, Yiting Shi, Jingyan Liu, Zhen Li. e-mail: yangshuhua@cau.edu.cn

附录

nature COMMUNICATIONS

ARTICLE

https://doi.org/10.1038/s41467-021-27690-x OPEN

The CLASSY family controls tissue-specific DNA methylation patterns in Arabidopsis

Ming Zhou[1,2], Ceyda Coruh[2], Guanghui Xu[2], Laura M. Martins[2], Clara Bourbousse[2,4], Alice Lambolez[2,5,6] & Julie A. Law[2,3]✉

DNA methylation shapes the epigenetic landscape of the genome, plays critical roles in regulating gene expression, and ensures transposon silencing. As is evidenced by the numerous defects associated with aberrant DNA methylation landscapes, establishing proper tissue-specific methylation patterns is critical. Yet, how such differences arise remains a largely open question in both plants and animals. Here we demonstrate that CLASSY1-4 (CLSY1-4), four locus-specific regulators of DNA methylation, also control tissue-specific methylation patterns, with the most striking pattern observed in ovules where CLSY3 and CLSY4 control DNA methylation at loci with a highly conserved DNA motif. On a more global scale, we demonstrate that specific *clsy* mutants are sufficient to shift the epigenetic landscape between tissues. Together, these findings reveal substantial epigenetic diversity between tissues and assign these changes to specific CLSY proteins, elucidating how locus-specific targeting combined with tissue-specific expression enables the CLSYs to generate epigenetic diversity during plant development.

[1] State Key Laboratory of Plant Physiology and Biochemistry, College of Life Sciences, Zhejiang University, Hangzhou 310058, China. [2] Plant Molecular and Cellular Biology Laboratory, Salk Institute for Biological Studies, La Jolla 92037, USA. [3] Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093, USA. [4] Present address: Institut de biologie de l'Ecole normale supérieure (IBENS), Ecole normale supérieure, CNRS, INSERM, PSL Université Paris, 75005 Paris, France. [5] Present address: RIKEN Center for Sustainable Resource Science, 1-7-22 Suehiro-cho, Tsurumi, Yokohama, Kanagawa 230-0045, Japan. [6] Present address: Department of Biological Sciences, Faculty of Science, The University of Tokyo, 7-3-1 Hongo, Bunkyō-ku, Tōkyō 113-8654, Japan. ✉email: jlaw@salk.edu

附录

nature COMMUNICATIONS

ARTICLE

https://doi.org/10.1038/s41467-022-29809-0 OPEN

A dirigent family protein confers variation of Casparian strip thickness and salt tolerance in maize

Yanyan Wang[1,5], Yibo Cao[1,2,5], Xiaoyan Liang[1], Junhong Zhuang[1,3], Xiangfeng Wang[4], Feng Qin[1,3] & Caifu Jiang[1,3]✉

Plant salt-stress response involves complex physiological processes. Previous studies have shown that some factors promote salt tolerance only under high transpiring condition, thus mediating transpiration-dependent salt tolerance (TDST). However, the mechanism underlying crop TDST remains largely unknown. Here, we report that *ZmSTL1* (*Salt-Tolerant Locus 1*) confers natural variation of TDST in maize. *ZmSTL1* encodes a dirigent protein (termed ZmESBL) localized to the Casparian strip (CS) domain. Mutants lacking ZmESBL display impaired lignin deposition at endodermal CS domain which leads to a defective CS barrier. Under salt condition, mutation of ZmESBL increases the apoplastic transport of Na^+ across the endodermis, and then increases the root-to-shoot delivery of Na^+ via transpiration flow, thereby leading to a transpiration-dependent salt hypersensitivity. Moreover, we show that the ortholog of ZmESBL also mediates CS development and TDST in Arabidopsis. Our study suggests that modification of CS barrier may provide an approach for developing salt-tolerant crops.

[1] State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, 100193 Beijing, China. [2] Key Laboratory of Forest Silviculture and Conservation of the Ministry of Education, College of Forestry, Beijing Forestry University, 100083 Beijing, China. [3] Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, 100193 Beijing, China. [4] National Maize Improvement Center of China, Department of Plant Genetics and Breeding, China Agricultural University, 100193 Beijing, China. [5] These authors contributed equally: Yanyan Wang, Yibo Cao. ✉email: cfjiang@cau.edu.cn

附录

nature COMMUNICATIONS

ARTICLE

https://doi.org/10.1038/s41467-022-28261-4 OPEN

Phloem iron remodels root development in response to ammonium as the major nitrogen source

Xing Xing Liu[1], Hai Hua Zhang[1], Qing Yang Zhu[1], Jia Yuan Ye[1], Ya Xin Zhu[1], Xiang Ting Jing[1], Wen Xin Du[1], Miao Zhou[1], Xian Yong Lin[1], Shao Jian Zheng[2] & Chong Wei Jin[1✉]

Plants use nitrate and ammonium as major nitrogen (N) sources, each affecting root development through different mechanisms. However, the exact signaling pathways involved in root development are poorly understood. Here, we show that, in *Arabidopsis thaliana*, either disruption of the cell wall-localized ferroxidase LPR2 or a decrease in iron supplementation efficiently alleviates the growth inhibition of primary roots in response to NH_4^+ as the N source. Further study revealed that, compared with nitrate, ammonium led to excess iron accumulation in the apoplast of phloem in an LPR2-dependent manner. Such an aberrant iron accumulation subsequently causes massive callose deposition in the phloem from a resulting burst of reactive oxygen species, which impairs the function of the phloem. Therefore, ammonium attenuates primary root development by insufficiently allocating sucrose to the growth zone. Our results link phloem iron to root morphology in response to environmental cues.

[1] State Key Laboratory of Plant Physiology and Biochemistry, College of Natural Resources and Environmental Science, Zhejiang University, Hangzhou 310058, China. [2] State Key Laboratory of Plant Physiology and Biochemistry, College of Life Science, Zhejiang University, Hangzhou 310058, China. ✉email: jincw@zju.edu.cn

PLANT SCIENCES

CPK28-NLP7 module integrates cold-induced Ca^{2+} signal and transcriptional reprogramming in *Arabidopsis*

Yanglin Ding[1]*†, Hao Yang[1]†, Shifeng Wu[1], Diyi Fu[1], Minze Li[1], Zhizhong Gong[1,2], Shuhua Yang[1]*

Exposure to cold triggers a spike in cytosolic calcium (Ca^{2+}) that often leads to transcriptional reprogramming in plants. However, how this Ca^{2+} signal is perceived and relayed to the downstream cold signaling pathway remains unknown. Here, we show that the CALCIUM-DEPENDENT PROTEIN KINASE 28 (CPK28) initiates a phosphorylation cascade to specify transcriptional reprogramming downstream of cold-induced Ca^{2+} signal. Plasma membrane (PM)–localized CPK28 is activated rapidly upon cold shock within 10 seconds in a Ca^{2+}-dependent manner. CPK28 then phosphorylates and promotes the nuclear translocation of NIN-LIKE PROTEIN 7 (NLP7), a transcription factor that specifies the transcriptional reprogramming of *cold-responsive* gene sets in response to Ca^{2+}, thereby positively regulating plant response to cold stress. This study elucidates a previously unidentified mechanism by which the CPK28-NLP7 regulatory module integrates cold-evoked Ca^{2+} signal and transcriptome and thus uncovers a key strategy for the rapid perception and transduction of cold signals from the PM to the nucleus.

INTRODUCTION

With climate change, temperature extremes are becoming more frequent, which have severe negative consequences on plant physiology and biochemistry. To survive, plants have evolved exquisite thermosensory systems to perceive and react to both low and high temperatures, thereby adapting their metabolism, growth, and architecture to their immediate environmental conditions.

Calcium (Ca^{2+}) is a ubiquitous and evolutionarily conserved second messenger that plays a critical role in cold responses of plants and animals (*1*, *2*). Cold induces the transient elevation of Ca^{2+} levels in the cytosol ($[Ca^{2+}]_{cyt}$) (referred to as the Ca^{2+} signature hereafter), a well-established phenomenon that is considered to be one of the earliest signaling events in response to cold (*1*, *2*). The channel TRANSIENT RECEPTOR POTENTIAL (TRP) MELASTATIN 8 (TRPM8) mediates the perception of cold and triggers a cold-induced Ca^{2+} signature in mouse (*Mus musculus*) (*3*, *4*). In plants, CHILLING TOLERANCE DIVERGENCE 1 (COLD1), a membrane-localized protein identified from rice (*Oryza sativa*), works together with G protein α subunit 1 (RGA1) to elicit the cold-induced Ca^{2+} influx and confers cold sensing, although the underlying mechanism is unknown (*5*). Several Ca^{2+} transporters and channels, including annexin 1 (AtANN1), MID1-COMPLEMENTING ACTIVITY 1 (MCA1), MCA2, and CYCLIC NUCLEOTIDE-GATED CHANNEL 9 (OsCNGC9), were shown to involve cold-evoked Ca^{2+} influx in *Arabidopsis* (*Arabidopsis thaliana*) and rice (*6*–*8*).

Pharmacological, genetic, and genomic evidence indicate that cold-induced Ca^{2+} signatures are likely perceived by putative Ca^{2+} sensors and decoded by downstream targets of the Ca^{2+} signal within cold regulatory networks, thereby resulting in transcriptional reprogramming in *Arabidopsis* (*9*). Members of the C-REPEAT BINDING FACTOR/DEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEIN 1 (CBF/DREB1) family are key transcription factors that act upstream of *COLD-RESPONSIVE* (*COR*) genes to induce their expression and promote cold tolerance (*10*, *11*). *Arabidopsis CBF* genes (*CBF1*–*CBF3*) are rapidly induced by cold stress (*12*), which is at least partially dependent on Ca^{2+} (*7*). Previous studies showed that the expression of *CBF* genes is indirectly modulated by Ca^{2+}/CALMODULIN-REGULATED RECEPTOR-LIKE KINASE 1/2 (CRLK1/2) (*13*, *14*) and directly regulated by the members of the CALMODULIN-BINDING TRANSCRIPTION ACTIVATOR (CAMTA) family of transcription factors (*15*, *16*). While the involvement of CRLK1/2 and CAMTAs in plant cold responses has been established, it is unclear whether they confer transcriptional reprogramming triggered by cold-induced Ca^{2+} signals.

Plants have three major families of calcium sensors: CALMODULIN (CaM), CALCINEURIN B-LIKE (CBL), and CALCIUM-DEPENDENT PROTEIN KINASES/CALCIUM-SENSOR PROTEIN KINASES (CDPKs/CPKs) (*17*). Unlike CaM and CBL that must relay Ca^{2+}-induced conformational changes to their partners for signaling, CPKs harbor four EF-hand Ca^{2+}-binding motifs and a Ser/Thr kinase domain that bring together both Ca^{2+} sensing and responding activity within a single protein (*18*). Therefore, Ca^{2+} signals can be directly converted into phosphorylation events within a single CPK protein. CPKs are encoded by a large gene family of 34 members in *Arabidopsis*, with overlapping and distinct expression patterns, whose encoded proteins exhibit both similar and different subcellular localizations and substrate specificity. CPKs therefore play versatile roles in triggering different downstream responses in plant immune, nitrate, and stress signaling networks (*19*, *20*). *Arabidopsis* CPK10, CPK30, and CPK32 are responsible for sensing and decoding a unique Ca^{2+} signal triggered by nitrate (*20*). OsCPK7 and OsCPK24 are themselves implicated in cold stress responses (*21*, *22*). However, which CPK acts as a Ca^{2+} sensor to sense and transmit the cold-induced Ca^{2+} signal remains elusive.

In this study, we report that cold shock rapidly activates the Ca^{2+}-dependent activity of CPK28 in plants. CPK28 phosphorylates the transcription factor NIN-LIKE PROTEIN 7 (NLP7), leading to its translocation from the cytosol to the nucleus in a Ca^{2+}-dependent

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China. [2]School of Life Science, Institute of Life Science and Green Development, Hebei University, Baoding, Hebei 071002, China.
*Corresponding author. Email: ding_yanglin@cau.edu.cn (Y.D.); yangshuhua@cau.edu.cn (S.Y.)
†These authors contributed equally to this work.

Developmental Cell

CellPress

Review

Surviving and thriving: How plants perceive and respond to temperature stress

Yanglin Ding[1,*] and Shuhua Yang[1,*]
[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
*Correspondence: yangshuhua@cau.edu.cn (S.Y.), ding_yanglin@cau.edu.cn (Y.D.)
https://doi.org/10.1016/j.devcel.2022.03.010

SUMMARY

The dramatic temperature fluctuations spurred by climate change inhibit plant growth and threaten crop productivity. Unraveling how plants defend themselves against temperature-stress-induced cellular impairment is not only a crucial fundamental issue but is also of critical importance for agricultural sustainability and food security. Here, we review recent developments in elucidating the molecular mechanisms used by plants to sense and respond to cold and heat stress at multiple levels. We also describe the trade-off between plant growth and responses to high and low temperatures. Finally, we discuss possible strategies that could be used to engineer temperature-stress-tolerant, high-yielding crops.

INTRODUCTION

Plants are increasingly subjected to cold and heat stress (referred to hereafter as "temperature stress") due to global warming and the accompanying extreme weather events. Temperature stress affects the geographical distribution of plants and reduces plant productivity, thus threatening food security. For example, for every 1°C increase in global average temperature, wheat, rice, maize, and soybean global yields will decrease by 6.0%, 3.2%, 7.4%, and 3.1% on average (Zhao et al., 2017a). Furthermore, in temperate areas, cold stress is responsible for approximately 30%–40% yield reductions in rice (Andaya and Mackill, 2003).

Plants have developed complex strategies for rapidly sensing and effectively responding to temperature stress. Theoretically, plants can rapidly sense temperature anywhere (e.g., plasma membrane [PM] and nucleus) in the cell, as temperature is a physical signal (Zhu, 2016). However, how plants perceive temperature signals remains a key fundamental question to be addressed. Plants can transmit heat or cold signals to cells in multiple ways, such as via calcium (Ca^{2+}) and reactive oxygen species (ROS) signaling and sustain cellular homeostasis and stability accordingly (Ding et al., 2020).

The activation of temperature-responsive genes is crucial for plant tolerance to temperature stress. These genes are regulated at multiple levels, including at the transcriptional and posttranscriptional levels (Ling et al., 2021; Shi et al., 2018; Ohama et al., 2017). For instance, C-REPEAT BINDING FACTOR/DEHYDRATION RESPONSIVE ELEMENT (DRE)-BINDING1 (CBF/DREB1) and HEAT SHOCK FACTOR A1 (HsfA1) are key transcription factors that directly activate the expression of *COLD-RESPONSIVE* (*COR*) and heat-responsive genes, respectively (Ohama et al., 2017; Thomashow, 1999). Alternative splicing (AS)-mediated gene expression is also important for temperature-stress tolerance (Ling et al., 2021). In addition, the transduction of temperature signals from organelles to the nucleus is critical for plant adaptation to temperature stress (Liu et al., 2020; Zhang et al., 2017; Deng et al., 2011).

Stress responses and growth inhibition are two complementary strategies that allow plants to efficiently defend themselves against stress (Zhang et al., 2020a). Cold-induced inhibition of growth is possible due to the reduced activities of enzymes and other proteins involved in cell expansion and cell division (Zhang et al., 2020a; Wang et al., 2017). Although beneficial for plant survival, active growth repression is often not conducive to high crop yields. Understanding the trade-off mechanism between growth and stress responses would lay the foundation for engineering stress-tolerant and high-yielding crops.

Here, we review recent progress in elucidating the roles of the major components involved in cold and heat signal sensing and response mechanisms. We focus on Ca^{2+} and ROS signaling and the regulation of gene expression, protein homeostasis, and protein activities. We also summarize recent advances in elucidating the trade-off between defense responses to temperature stress and plant growth. Finally, we propose potential strategies to breed heat- or cold-tolerant crops and discuss the unique challenges that might be faced.

Sensing temperature stress signals

The cell membrane represents the first line of defense against temperature stress and is therefore likely the primary site for sensing temperature signals (Ding et al., 2019b). Accumulating evidence suggests that the nucleus is also an important organelle in temperature sensing.

Sensing at the cell membrane

Both cold and heat stress can alter the fluidity of cellular phospholipid membranes. Changes in cell-membrane fluidity and membrane lipid composition are essential for plant cold and heat tolerance, as demonstrated in pharmacological and genetic assays (Ding et al., 2019b). Changes in cell-membrane fluidity might be sensed by membrane-localized proteins

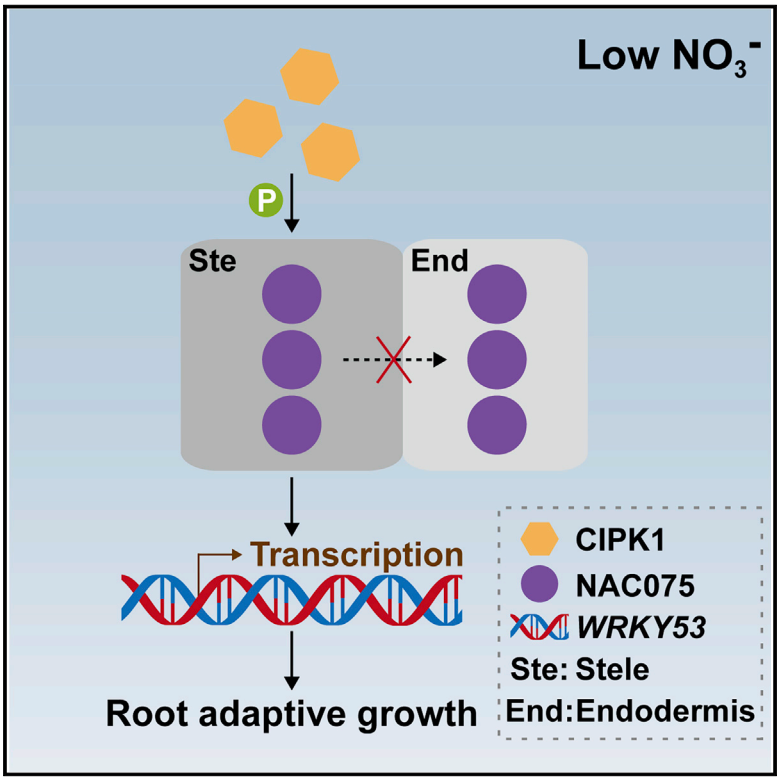
附录

Article

Developmental Cell

Nitrate availability controls translocation of the transcription factor NAC075 for cell-type-specific reprogramming of root growth

Graphical abstract



Authors

Huixin Xiao, Yumei Hu, Yaping Wang, ..., Zhizhong Gong, Jiří Friml, Jing Zhang

Correspondence

zhangj@cau.edu.cn

In brief

To face changing nutrient availability in the soil, plants have to optimize their root systems accordingly. Xiao et al. identify an adaptive mechanism involving transcription factor translocation based on nutrient availability and cell-specific reprogramming that modulates plant root development.

Highlights

- *lonr1* defective in *NAC075* is hyposensitive to low NO_3^- in primary root growth
- NAC075 moves from root stele tissue to endodermal layer based on NO_3^- availability
- NAC075 relocation relies on CIPK1-mediated phosphorylation and is vital for root growth
- *WRKY53* acts as a downstream target of NAC075 to regulate root responses to low NO_3^-

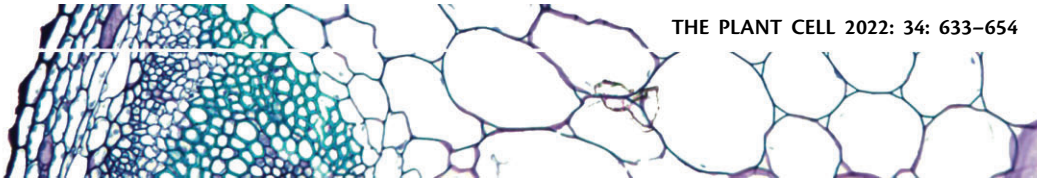
Xiao et al., 2022, Developmental Cell *57*, 2638–2651
December 5, 2022
https://doi.org/10.1016/j.devcel.2022.11.006

CellPress

doi:10.1093/plcell/koab254

THE PLANT CELL

THE PLANT CELL 2022: 34: 633–654



Research Article

Mutual upregulation of HY5 and TZP in mediating phytochrome A signaling

Cong Li [1,†] Lijuan Qi [1,†] Shaoman Zhang [1] Xiaojing Dong [1] Yanjun Jing [2] Jinkui Cheng [1] Ziyi Feng [1] Jing Peng [1] Hong Li [1] Yangyang Zhou [1] Xiaoji Wang [1] Run Han [1] Jie Duan [1] William Terzaghi [3] Rongcheng Lin [2] and Jigang Li [1,*,‡]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 Key Laboratory of Photobiology, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
3 Department of Biology, Wilkes University, Wilkes-Barre, Pennsylvania 18766, USA

*Author for correspondence: jigangli@cau.edu.cn
†These authors contributed equally (C.L., L.Q.).
‡Senior author.

J.L., C.L., and L.Q. designed research. C.L., L.Q., S.Z., X.D., Y.J., Z.F., H.L., Y.Z., X.W., R.H., J.P., and J.D. performed research. J.C. analyzed the RNA-sequencing data. J.L. and R.L. discussed and interpreted the data. J.L., C.L., L.Q., and W.T. wrote the paper.
The author responsible for the distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Jigang Li (jigangli@cau.edu.cn).

Abstract

Phytochrome A (phyA) is the far-red (FR) light photoreceptor in plants that is essential for seedling de-etiolation under FR-rich environments, such as canopy shade. TANDEM ZINC-FINGER/PLUS3 (TZP) was recently identified as a key component of phyA signal transduction in *Arabidopsis thaliana*; however, how TZP is integrated into the phyA signaling networks remains largely obscure. Here, we demonstrate that ELONGATED HYPOCOTYL5 (HY5), a well-characterized transcription factor promoting photomorphogenesis, mediates FR light induction of *TZP* expression by directly binding to a G-box motif in the *TZP* promoter. Furthermore, TZP physically interacts with CONSTITUTIVE PHOTOMORPHOGENIC1 (COP1), an E3 ubiquitin ligase targeting HY5 for 26S proteasome-mediated degradation, and this interaction inhibits COP1 interaction with HY5. Consistent with those results, TZP post-translationally promotes HY5 protein stability in FR light, and in turn, TZP protein itself is destabilized by COP1 in both dark and FR light conditions. Moreover, *tzp hy5* double mutants display an additive phenotype relative to their respective single mutants under high FR light intensities, indicating that TZP and HY5 also function in largely independent pathways. Together, our data demonstrate that HY5 and TZP mutually upregulate each other in transmitting the FR light signal, thus providing insights into the complicated but delicate control of phyA signaling networks.

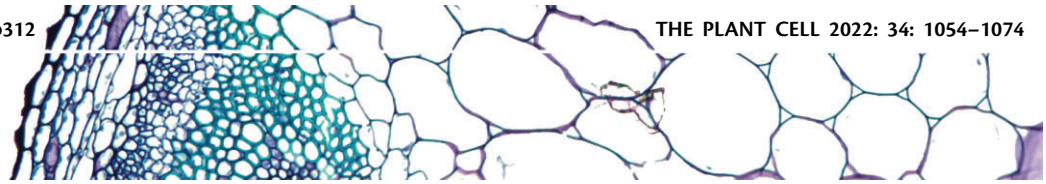
Introduction

Plant canopy shade is enriched in far-red (FR) light because the red (R; 600–700 nm) and blue (B; 400–500 nm) wavelengths of sunlight are absorbed by chlorophyll and carotenoid pigments of upper leaves, while FR wavelengths (700–750 nm) are transmitted or reflected by plant tissues (Casal, 2013; Fiorucci and Fankhauser, 2017; Legris et al., 2019). Plants use the phytochrome family of photoreceptors to perceive the R and FR components of their light environment, and phytochromes are widely conserved in seed plants and nonseed plants including ferns, mosses, and charophyte algae (Li et al., 2011, 2015; Rensing et al., 2016; Paik

Received August 10, 2021. Accepted October 08, 2021. Advance access publication November 6, 2021

附录

http://doi.org/10.1093/plcell/koab312 THE PLANT CELL 2022: 34: 1054–1074



Research Article

ENB1 encodes a cellulose synthase 5 that directs synthesis of cell wall ingrowths in maize basal endosperm transfer cells

Qun Wang [1], Mingmin Wang [2], Jian Chen [1], Weiwei Qi [2], Jinsheng Lai [1], Zeyang Ma [1] and Rentao Song [1,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center, Beijing Key Laboratory of Crop Genetic Improvement, Joint International Research Laboratory of Crop Molecular Breeding, College of Agronomy and Biotechnology, China Agricultural University, Beijing 100193, China

2 Shanghai Key Laboratory of Bio-Energy Crops, Plant Science Center, School of Life Sciences, Shanghai University, Shanghai 200444, China

*Author for correspondence: rentaosong@cau.edu.cn

†Senior author.

R.S. conceived the project and designed the experiments. Q.W. and M.W. performed the experiments. All authors analyzed the data. Q.W. and R.S. wrote the manuscript.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Rentao Song (rentaosong@cau.edu.cn).

Abstract

Development of the endosperm is strikingly different in monocots and dicots: it often manifests as a persistent tissue in the former and transient tissue in the latter. Little is known about the controlling mechanisms responsible for these different outcomes. Here we characterized a maize (*Zea mays*) mutant, *endosperm breakdown1* (*enb1*), in which the typically persistent endosperm (PE) was drastically degraded during kernel development. *ENB1* encodes a cellulose synthase 5 that is predominantly expressed in the basal endosperm transfer layer (BETL) of endosperm cells. Loss of ENB1 function caused a drastic reduction in formation of flange cell wall ingrowths (ingrowths) in BETL cells. Defective ingrowths impair nutrient uptake, leading to premature utilization of endosperm starch to nourish the embryo. Similarly, developing wild-type kernels cultured in vitro with a low level of sucrose manifested early endosperm breakdown. *ENB1* expression is induced by sucrose via the BETL-specific Myb-Related Protein1 transcription factor. Overexpression of *ENB1* enhanced development of flange ingrowths, facilitating sucrose transport into BETL cells and increasing kernel weight. The results demonstrated that ENB1 enhances sucrose supply to the endosperm and contributes to a PE in the kernel.

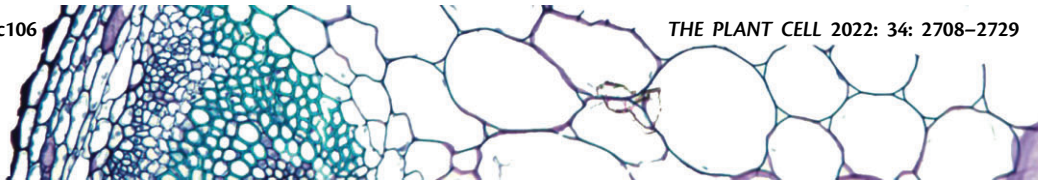
Introduction

The angiosperm seed contains two zygotic components, the endosperm, and the embryo, and their development is distinctly different in monocots and dicots. Generally, in monocots such as maize (*Zea mays*), the endosperm is a persistent tissue that accumulates large amounts of nutrient reserves, primarily starch, and ultimately occupies the largest portion of the mature seed (Olsen, 2004; Sabelli and Larkins, 2009). In contrast, in dicots, such as Arabidopsis (*Arabidopsis thaliana*), the endosperm is a transient tissue and is largely consumed during embryo development, leaving one layer of cells at maturation (Li and Berger, 2012; Sreenivasulu and Wobus, 2013; Grimault et al., 2015).

Received September 13, 2021. Accepted November 27, 2021. Advance access publication December 22, 2021

附录

https://doi.org/10.1093/plcell/koac106 THE PLANT CELL 2022: 34: 2708–2729



Research Article

Phosphorylation of the plasma membrane H^+-ATPase AHA2 by BAK1 is required for ABA-induced stomatal closure in Arabidopsis

Dan Pei [1], Deping Hua [2], Jinping Deng [1], Zhifang Wang [1], Chunpeng Song [3], Yi Wang [1], Yu Wang [1], Junsheng Qi [1], Hannes Kollist [4], Shuhua Yang [1], Yan Guo [1] and Zhizhong Gong [1,5,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 School of Life Sciences, Tianjin University, Tianjin 300072, China
3 Collaborative Innovation Center of Crop Stress Biology, Institute of Plant Stress Biology, Henan University, Kaifeng 475001, China
4 Plant Signal Research Group, Institute of Technology, University of Tartu, Tartu 50411, Estonia
5 School of Life Sciences, Institute of Life Science and Green Development, Hebei University, Baoding 071002, China

*Author for correspondence: gongzz@cau.edu.cn
†Senior author

Z.G. and P.D. designed research. P.D. and D.H. performed research. P.D., Z.G., J.D., Z.W., D.H., and Y.G. analyzed data, and P.D. and Z.G. wrote the paper. All authors discussed and interpreted the data.
The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Zhizhong Gong (gongzz@cau.edu.cn).

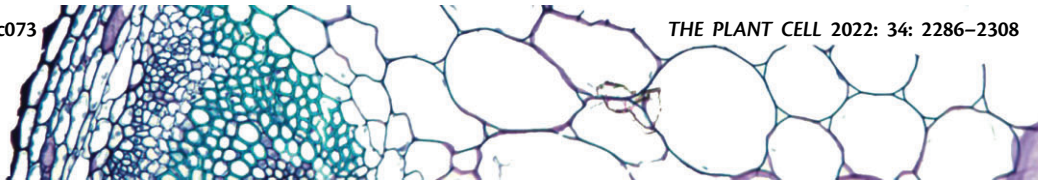
Abstract

Stomatal opening is largely promoted by light-activated plasma membrane-localized proton ATPases (PM H^+-ATPases), while their closure is mainly modulated by abscisic acid (ABA) signaling during drought stress. It is unknown whether PM H^+-ATPases participate in ABA-induced stomatal closure. We established that BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) interacts with, phosphorylates and activates the major PM Arabidopsis H^+-ATPase isoform 2 (AHA2). Detached leaves from *aha2-6* single mutant *Arabidopsis thaliana* plants lost as much water as *bak1-4* single and *aha2-6 bak1-4* double mutants, with all three mutants losing more water than the wild-type (Columbia-0 [Col-0]). In agreement with these observations, *aha2-6*, *bak1-4*, and *aha2-6 bak1-4* mutants were less sensitive to ABA-induced stomatal closure than Col-0, whereas the *aha2-6* mutation did not affect ABA-inhibited stomatal opening under light conditions. ABA-activated BAK1 phosphorylated AHA2 at Ser-944 in its C-terminus and activated AHA2, leading to rapid H^+ efflux, cytoplasmic alkalinization, and reactive oxygen species (ROS) accumulation, to initiate ABA signal transduction and stomatal closure. The phosphorylation-mimicking mutation $AHA2^{S944D}$ driven by its own promoter could largely compensate for the defective phenotypes of water loss, cytoplasmic alkalinization, and ROS accumulation in both *aha2-6* and *bak1-4* mutants. Our results uncover a crucial role of AHA2 in cytoplasmic alkalinization and ABA-induced stomatal closure during the plant's response to drought stress.

Received January 18, 2022. Accepted April 4, 2022. Advance access publication April 11, 2022

附录

https://doi.org/10.1093/plcell/koac073 THE PLANT CELL 2022: 34: 2286–2308



Research Article

COP1 positively regulates ABA signaling during Arabidopsis seedling growth in darkness by mediating ABA-induced ABI5 accumulation

Jing Peng [1], Meijiao Wang [1], Xiaoji Wang [1], Lijuan Qi [1], Can Guo [1], Hong Li [1], Cong Li [1], Yan Yan [1], Yun Zhou [2], William Terzaghi [3], Zhen Li [1], Chun-Peng Song [2], Feng Qin [1], Zhizhong Gong [1] and Jigang Li [1,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 State Key Laboratory of Crop Stress Adaptation and Improvement, Collaborative Innovation Center of Crop Stress Biology, Henan University, Kaifeng 475004, China
3 Department of Biology, Wilkes University, Wilkes-Barre, Pennsylvania 18766, USA

*Author for correspondence: jigangli@cau.edu.cn
†Senior author.

J.L. and J.P. designed the research; J.P., M.W., X.W., L.Q., C.G., H.L., C.L., Y.Y., and Z.L. performed the research; J.L., Z.G., F.Q., C.-P.S. and Y.Z. analyzed the data; and J.L., J.P., and W.T. wrote the paper.
The author responsible for the distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Jigang Li (jigangli@cau.edu.cn).

Abstract

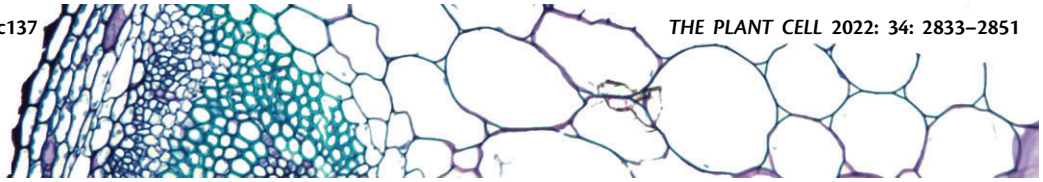
CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), a well-characterized E3 ubiquitin ligase, is a central repressor of seedling photomorphogenic development in darkness. However, whether COP1 is involved in modulating abscisic acid (ABA) signaling in darkness remains largely obscure. Here, we report that COP1 is a positive regulator of ABA signaling during Arabidopsis seedling growth in the dark. COP1 mediates ABA-induced accumulation of ABI5, a transcription factor playing a key role in ABA signaling, through transcriptional and post-translational regulatory mechanisms. We further show that COP1 physically interacts with ABA-hypersensitive DCAF1 (ABD1), a substrate receptor of the CUL4-DDB1 E3 ligase targeting ABI5 for degradation. Accordingly, COP1 directly ubiquitinates ABD1 in vitro, and negatively regulates ABD1 protein abundance in vivo in the dark but not in the light. Therefore, COP1 promotes ABI5 protein stability post-translationally in darkness by destabilizing ABD1 in response to ABA. Interestingly, we reveal that ABA induces the nuclear accumulation of COP1 in darkness, thus enhancing its activity in propagating the ABA signal. Together, our study uncovers that COP1 modulates ABA signaling during seedling growth in darkness by mediating ABA-induced ABI5 accumulation, demonstrating that plants adjust their ABA signaling mechanisms according to their light environment.

Introduction

Plants have evolved a remarkable ability to survive abiotic stresses. The phytohormone abscisic acid (ABA) rapidly accumulates in response to environmental stresses such as drought, cold, or salinity, and plays important roles in plant adaptation to these stresses (Cutler et al., 2010; Finkelstein, 2013; Li et al., 2017; Chen et al., 2020). Therefore, ABA has long been regarded as a "stress hormone". However, ABA also clearly regulates additional aspects of plant growth and development, including seed maturation and dormancy,

Received July 21, 2021. Accepted February 8, 2022. Advance access publication February 28, 2022

https://doi.org/10.1093/plcell/koac137 THE PLANT CELL 2022: 34: 2833–2851



Research Article

The transcription factor *bZIP68* negatively regulates cold tolerance in maize

Zhuoyang Li ,[1] Diyi Fu ,[1] Xi Wang ,[1] Rong Zeng,[1] Xuan Zhang ,[2] Jinge Tian ,[2] Shuaisong Zhang ,[1] Xiaohong Yang ,[2] Feng Tian ,[2] Jinsheng Lai ,[2] Yiting Shi [1,*] and Shuhua Yang [1,*]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China
2 State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center, Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China

*Author for correspondence: shiyiting@cau.edu.cn (Y.S.), yangshuhua@cau.edu.cn (S.Y.)

S.Y. conceived the project. Y.S. and S.Y. designed the experiments. Z.L. and Y.S. performed most of the experiments. Z.L. and D.F. performed the RNA-seq analysis. S.Z. performed the maize transformation. Z.L., X.Z., and J.T. peformed the maize domestication analysis. Z.L., X.W., R.Z., X.Y., F.T., J.L., Y.S., and S.Y. analyzed and discussed the data. Z.L., Y.S., and S.Y. wrote the manuscript with comments from all the authors.
The authors responsible for distribution for materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) are: Yiting Shi (shiyiting@cau.edu.cn) and Shuhua Yang (yangshuhua@cau.edu.cn).

Abstract

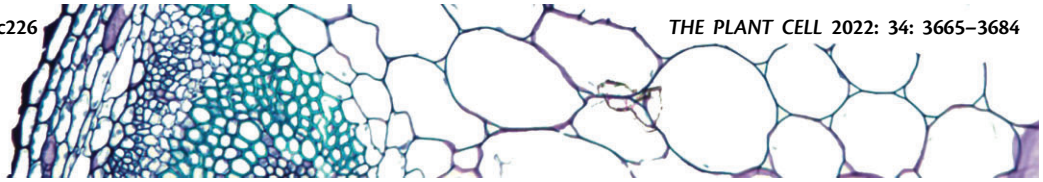
Maize (*Zea mays*) originated in tropical areas and is thus susceptible to low temperatures, which pose a major threat to maize production. Our understanding of the molecular basis of cold tolerance in maize is limited. Here, we identified bZIP68, a basic leucine zipper (bZIP) transcription factor, as a negative regulator of cold tolerance in maize. Transcriptome analysis revealed that bZIP68 represses the cold-induced expression of *DREB1* transcription factor genes. The stability and transcriptional activity of bZIP68 are controlled by its phosphorylation at the conserved Ser250 residue under cold stress. Furthermore, we demonstrated that the *bZIP68* locus was a target of selection during early domestication. A 358-bp insertion/deletion (Indel-972) polymorphism in the *bZIP68* promoter has a significant effect on the differential expression of *bZIP68* between maize and its wild ancestor teosinte. This study thus uncovers an evolutionary cis-regulatory variant that could be used to improve cold tolerance in maize.

Introduction

Cold stress is a major environmental factor that severely constrains the growth, development, and geographical distribution of crops in nature (Sobkowiak et al., 2016). The adverse effects of cold stress on plants affect many aspects of physiology and biochemistry, including photosynthesis, respiration, enzymatic reactions, carbon/nitrogen (C/N) balance, secondary metabolism, and nutrient absorption. Exposure to colder temperatures may therefore lead to poor germination, stunted seedling growth, and even the death of tissues or entire plants, which lowers crop quality and delays harvest and may even result in crop failure (Allen and Ort, 2001; Marocco et al., 2005; Nguyen et al., 2009; Hussain et al., 2020). Maize (*Zea mays*) is a major food crop that has adapted to a wide range of environmental conditions worldwide. However, because it originated at tropical latitudes,

Received December 06, 2021. Accepted April 22, 2022. Advance access publication May 11, 2022

https://doi.org/10.1093/plcell/koac226 THE PLANT CELL 2022: 34: 3665–3684



Research Article

Arabidopsis ERdj3B coordinates with ERECTA-family receptor kinases to regulate ovule development and the heat stress response

Ya-Jun Leng [1], Ya-Sen Yao [1], Ke-Zhen Yang [2,3], Pei-Xiang Wu [1], Yu-Xin Xia [1], Chao-Ran Zuo [2,3], Jing-Hong Luo [1], Pu Wang [1], Yang-Yang Liu [1], Xue-Qin Zhang [1], De Ye [1], Jie Le [2,3] and Li-Qun Chen [1,*]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 Key Laboratory of Plant Molecular Physiology, CAS Center for Excellence in Molecular Plant Sciences, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
3 University of Chinese Academy of Sciences, Beijing 100049, China

*Author for correspondence: chenliqun@cau.edu.cn
These authors contributed equally (Y.-J.L., Y.-S.Y., and K.-Z.Y.)

Y.-J.L. and L.-Q.C. conceived and designed the experiments. Y.-J.L., Y.-S.Y., P.-X.W., Y.-X.X., P.W., and Y.-Y.L. performed the experiments. K.-Z.Y., C.-R.Z., and J.L. provided some of the materials and performed some of the experiments. J.-H.L. and X.-Q.Z. helped analyze the data. Y.-J.L., D.Y., and L.-Q.C. wrote the article.
The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Li-Qun Chen (chenliqun@cau.edu.cn).

Abstract

The endoplasmic reticulum-localized DnaJ family 3B (ERdj3B), is a component of the stromal cell-derived factor 2 (SDF2)–ERdj3B–binding immunoglobulin protein (BiP) chaperone complex, which functions in protein folding, translocation, and quality control. We found that *ERdj3B* mutations affected integument development in the L*er* ecotype but not in the Col-0 ecotype of Arabidopsis (*Arabidopsis thaliana*). Map-based cloning identified the *ERECTA* (*ER*) gene as a natural modifier of *ERdj3B*. The double mutation of *ERdj3B* and *ER* caused a major defect in the inner integument under heat stress. Additional mutation of the *ER* paralog *ERECTA-LIKE 1* (*ERL1*) or *ERL2* to the *erdj3b er* double mutant exacerbated the defective integument phenotype. The double mutation of *ER* and *SDF2*, the other component of the SDF2–ERdj3B–BiP complex, resulted in similar defects in the inner integument. Furthermore, both the protein abundance and plasma membrane partitioning of ER, ERL1, and ERL2 were markedly reduced in *erdj3b* plants, indicating that the SDF2–ERdj3B–BiP chaperone complex might control the translocation of ERECTA-family proteins from the endoplasmic reticulum to the plasma membrane. Our results suggest that the SDF2–ERdj3B–BiP complex functions in ovule development and the heat stress response in coordination with ERECTA-family receptor kinases.

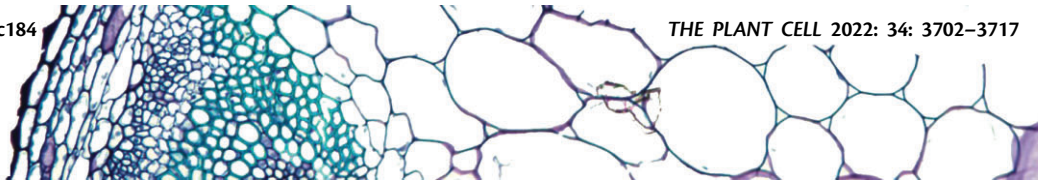
Introduction

The ovule, which develops into a seed after fertilization, is an important component of the female reproductive system in angiosperms. During ovule development, three elements are laid down along the proximal–distal axis: the nucellus at the distal end (harboring the megaspore/gametophyte lineage), the chalaza (flanked by the integuments), and the funiculus at the proximal end (Schneitz et al., 1995). The

Received March 24, 2022. Accepted July 21, 2022. Advance access publication July 28, 2022

附录

https://doi.org/10.1093/plcell/koac184 THE PLANT CELL 2022: 34: 3702–3717



Research Article

Heat shock protein 101 contributes to the thermotolerance of male meiosis in maize

Yunfei Li [1,3], Yumin Huang [1,3], Huayue Sun [4], Tianyi Wang [1,3], Wei Ru [1,3], Lingling Pan [1,3], Xiaoming Zhao [3], Zhaobin Dong [1,3], Wei Huang [1,3,*] and Weiwei Jin [1,2,3,*]

1 State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center of China, Beijing Key Laboratory of Crop Genetic Improvement, Key Laboratory of Crop Heterosis and Utilization, Ministry of Education, China Agricultural University, Beijing 100193, China
2 College of Agronomy and Resources and Environment, Tianjin Agricultural University, Tianjin 300384, China
3 Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China
4 College of Plant Protection, Henan Agricultural University, Zhengzhou 450002, China

*Author for correspondence: wilsonhuang23@cau.edu.cn (W.H.), weiweijin@cau.edu.cn (W.J.)

W.J., Y.L., and W.H. designed the project. Y.L., H.S., T.W., L.P., and X.Z. performed the experiments. Y.L., Y.H., and W.R. analyzed the data and generated graphs. Y.L., W.J., W.H., and Z.D. wrote the manuscript.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Weiwei Jin (weiweijin@cau.edu.cn).

Abstract

High temperatures interfere with meiotic recombination and the subsequent progression of meiosis in plants, but few genes involved in meiotic thermotolerance have been characterized. Here, we characterize a maize (*Zea mays*) classic dominant male-sterile mutant *Ms42*, which has defects in pairing and synapsis of homologous chromosomes and DNA double-strand break (DSB) repair. *Ms42* encodes a member of the heat shock protein family, HSP101, which accumulates in pollen mother cells. Analysis of the dominant *Ms42* mutant and *hsp101* null mutants reveals that HSP101 functions in RADIATION SENSITIVE 51 loading, DSB repair, and subsequent meiosis. Consistent with these functions, overexpression of *Hsp101* in anthers results in robust microspores with enhanced heat tolerance. These results demonstrate that HSP101 mediates thermotolerance during microsporogenesis, shedding light on the genetic basis underlying the adaptation of male meiocytes to high temperatures.

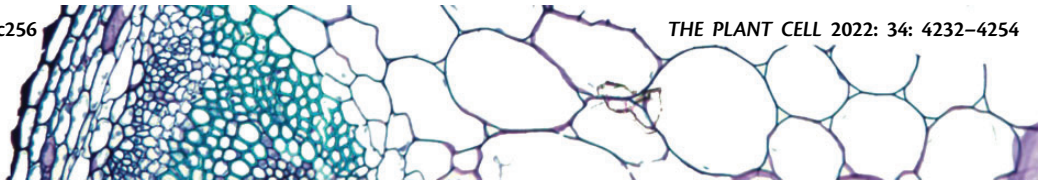
Introduction

Meiosis, the basis of sexual reproduction, plays a critical role in genome diversity and ploidy stability in plants. Appropriate chromosome segregation in meiosis relies on a series of highly coordinated events during prophase I, including homologous chromosome pairing, synapsis, and recombination (Zickler and Kleckner, 2015). Meiotic recombination (MR) is initiated by the programmed introduction of DNA double-strand breaks (DSBs), which is catalyzed by conserved type-II topoisomerase-like enzyme sporulation protein 11 and a group of accessory proteins (Keeney et al., 1997; Grelon et al., 2001). Following that, programmed DSB ends are processed by the MRX/N (Mre11-Rad50-Xrs2/Nbs1) and Sae2/Com1/CtIP/Ctp1 protein complex into single-stranded DNA tails (Borde, 2007). Then RADIATION SENSITIVE 51 (RAD51) and DISRUPTED MEIOTIC CDNA 1 are loaded onto the single-stranded DNA to facilitate homologous searching and single-

Received February 15, 2022. Accepted June 17, 2022. Advance access publication June 27, 2022

附录

https://doi.org/10.1093/plcell/koac256 THE PLANT CELL 2022: 34: 4232–4254



Research Article

The sugar transporter ZmSUGCAR1 of the nitrate transporter 1/peptide transporter family is critical for maize grain filling

Bo Yang [1], Jing Wang [1], Miao Yu [2], Meiling Zhang [1], Yanting Zhong [3], Tianyi Wang [4], Peng Liu [5], Weibin Song[1], Haiming Zhao [1], Astrid Fastner [6], Marianne Suter[6], Doris Rentsch [6], Uwe Ludewig [7], Weiwei Jin [4,8], Dietmar Geiger [9], Rainer Hedrich [9], David M. Braun [10], Karen E. Koch [5], Donald R. McCarty [5], Wei-Hua Wu [2,8], Xuexian Li [3,8,*], Yi Wang [2,8,*] and Jinsheng Lai [1,8,*]

1 State Key Laboratory of Plant Physiology and Biochemistry (SKLPPB) and National Maize Improvement Center, Department of Plant Genetics and Breeding, China Agricultural University, Beijing 100193, China
2 State Key Laboratory of Plant Physiology and Biochemistry (SKLPPB), College of Biological Sciences, China Agricultural University, Beijing 100193, China
3 The Key Laboratory of Plant–Soil Interactions (MOE), Department of Plant Nutrition, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China
4 National Maize Improvement Center, Department of Plant Genetics and Breeding, China Agricultural University, Beijing 100193, China
5 Plant Molecular and Cellular Biology Program, Horticultural Sciences Department, Genetics Institute, University of Florida, Gainesville, Florida, USA
6 Institute of Plant Sciences, University of Bern, Bern 3013, Switzerland
7 Institute of Crop Science, Nutritional Crop Physiology (340h), University of Hohenheim, Stuttgart 70593, Germany
8 Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China
9 Department of Molecular Plant Physiology and Biophysics, Julius-von-Sachs-Institute for Biosciences, University of Würzburg, Würzburg 97082, Germany
10 Division of Biological Sciences, Interdisciplinary Plant Group, and Missouri Maize Center, University of Missouri, 116 Tucker Hall, Columbia, Missouri 65211, USA

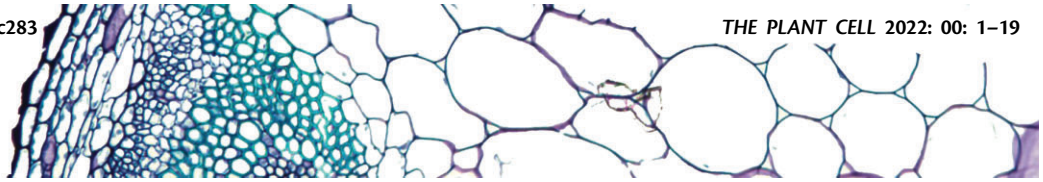
*Author for correspondence: jlai@cau.edu.cn (J.L.), yiwang@cau.edu.cn (Y.W.), steve@cau.edu.cn (X.L.)
These authors contributed equally (B.Y., J.W., M.Y., and M.Z.)
J.L., B.Y., Y.W., and J.W. designed the research. B.Y., J.W., M.Y., M.Z., Y.Z., T.W., P.L., W.S., H.Z., A.F., and M.S. conducted the experiments. B.Y., J.L., Y.W., and X.L. wrote the article. R.H., D.G., W.-H.W., D.R., U.L., W.J., D.M.B., K.E.K., and D.R.M. revised the article.
The author(s) responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) are: Jinsheng Lai (jlai@cau.edu.cn), Yi Wang (yiwang@cau.edu.cn), Xuexian Li (steve@cau.edu.cn)

Abstract

Maternal-to-filial nutrition transfer is central to grain development and yield. nitrate transporter 1/peptide transporter (NRT1-PTR)-type transporters typically transport nitrate, peptides, and ions. Here, we report the identification of a maize (*Zea mays*) NRT1-PTR-type transporter that transports sucrose and glucose. The activity of this sugar transporter, named Sucrose and Glucose Carrier 1 (SUGCAR1), was systematically verified by tracer-labeled sugar uptake and serial electrophysiological studies including two-electrode voltage-clamp, non-invasive microelectrode ion flux estimation assays in *Xenopus laevis* oocytes and patch clamping in HEK293T cells. *ZmSUGCAR1* is specifically expressed in the basal endosperm transfer layer and loss-of-function mutation of *ZmSUGCAR1* caused significantly decreased sucrose and glucose contents and

Received December 17, 2021. Accepted July 31, 2022. Advance access publication September 1, 2022

https://doi.org/10.1093/plcell/koac283 THE PLANT CELL 2022: 00: 1–19



Research Article

SALT OVERLY SENSITIVE 1 is inhibited by clade D Protein phosphatase 2C D6 and D7 in *Arabidopsis thaliana*

Haiqi Fu ,[1] **Xiang Yu** ,[1] **Yuanyuan Jiang** ,[1] **Yuhan Wang** ,[1] **Yongqing Yang** ,[1] **She Chen** ,[2] **Qijun Chen** [1] and **Yan Guo** [1,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 National Institute of Biological Sciences, Beijing 100093, China

*Author for correspondence: guoyan@cau.edu.cn
†Senior author.

H.F. and Y.G. designed the study. H.F. performed the experiments. H.F., X.Y., Y.J, Y.W., and Y.G. analyzed the data. H.F. and Y.G. wrote the paper.
The author(s) responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Yan Guo (guoyan@cau.edu.cn)

Abstract

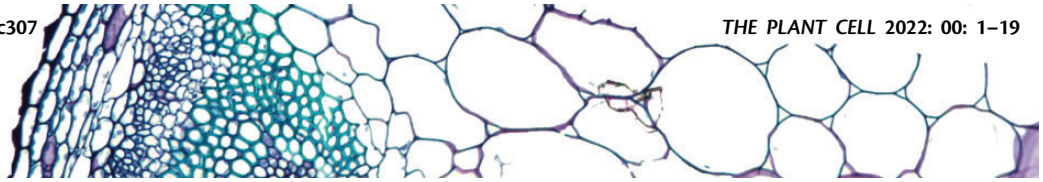
The salt overly sensitive (SOS) pathway is essential for maintaining sodium ion homeostasis in plants. This conserved pathway is activated by a calcium signaling-dependent phosphorylation cascade. However, the identity of the phosphatases and their regulatory mechanisms that would deactivate the SOS pathway remain unclear. In this study, we demonstrate that PP2C.D6 and PP2C.D7, which belong to clade D of the protein phosphatase 2C (PP2C) subfamily in *Arabidopsis thaliana*, directly interact with SOS1 and inhibit its Na^+/H^+ antiporter activity under non-salt-stress conditions. Upon salt stress, SOS3-LIKE CALCIUM-BINDING PROTEIN8 (SCaBP8), a member of the SOS pathway, interacts with the PP2Cs and suppresses their phosphatase activity; simultaneously, SCaBP8 regulates the subcellular localization of PP2C.D6 by releasing it from the plasma membrane. Thus, we identified two negative regulators of the SOS pathway that repress SOS1 activity under nonstress conditions. These processes set the stage for the activation of SOS1 by the kinase SOS2 to achieve plant salt tolerance. Our results suggest that reversible phosphorylation/dephosphorylation is crucial for the regulation of the SOS pathway, and that calcium sensors play dual roles in activating/deactivating SOS2 and PP2C phosphatases under salt stress.

Introduction

Soil salinity is an important abiotic stress limiting crop production and land usage (Gong et al., 2020). Salt stress induces ionic stress, osmotic stress, and secondary stresses such as oxidative stress in plants (Yang and Guo, 2018b). The salt overly sensitive (SOS) pathway, which is conserved in plants, transports intracellular Na^+ out of the cytoplasm under salt stress conditions (Zhu, 2002; Yang and Guo, 2018b). There are four major components in the SOS pathway: two calcium-binding proteins, SOS3 and SOS3-LIKE CALCIUM-BINDING PROTEIN 8 (SCaBP8, also named Calcineurin B-Like10 [CBL10]); the protein kinase SOS2; and the plasma membrane Na^+/H^+ antiporter SOS1 (Zhu, 2000; Yang and Guo, 2018a). Under salt stress, Ca^{2+} concentrations increase in the cytosol. SOS3 and SCaBP8 perceive this calcium signal, interact with the FISL motif at the C-terminus of SOS2 to activate its kinase activity, and recruit SOS2 to the plasma membrane. SOS2 then phosphorylates the S1136 and S1138 residues in the C-terminal auto-inhibitory domain of SOS1 to activate its Na^+/H^+

Received June 17, 2022. Accepted September 08, 2022. Advance access publication September 23, 2022

https://doi.org/10.1093/plcell/koac307 THE PLANT CELL 2022: 00: 1–19



Research Article

The OPEN STOMATA1–SPIRAL1 module regulates microtubule stability during abscisic acid-induced stomatal closure in Arabidopsis

Pan Wang [1], Sijia Qi [1], Xiaohong Wang [1], Liru Dou [1], Meng-ao Jia [2], Tonglin Mao [1], Yushuang Guo [2,*] and Xiangfeng Wang [1,*]

1 State Key Laboratory of Plant Physiology and Biochemistry, Department of Plant Sciences, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 Key Laboratory of Molecular Genetics, Guizhou Academy of Tobacco Science, Guiyang 550081, China

*Authors for correspondence: yshguo@126.com (Y.G.), wangxf2017@cau.edu.cn (X.F.W.)
These authors contributed equally (P.W. and S.Q.)
X.F.W. and T.M. designed the experiments. P.W., S.Q., X.H.W., and L.D. performed the experiments. P.W., S.Q., and X.F.W. analyzed the data. M.J., Y.G., and X.F.W. wrote and revised the manuscript.
The author responsible for the distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell) is: Xiangfeng Wang (wangxf2017@cau.edu.cn).

Abstract

Drought stress triggers abscisic acid (ABA) signaling in guard cells and induces stomatal closure to prevent water loss in land plants. Stomatal movement is accompanied by reorganization of the cytoskeleton. Cortical microtubules disassemble in response to ABA, which is required for stomatal closure. However, how ABA signaling regulates microtubule disassembly is unclear, and the microtubule-associated proteins (MAPs) involved in this process remain to be identified. In this study, we show that OPEN STOMATA 1 (OST1), a central component in ABA signaling, mediates microtubule disassembly during ABA-induced stomatal closure in *Arabidopsis thaliana*. We identified the MAP SPIRAL1 (SPR1) as the substrate of OST1. OST1 interacts with and phosphorylates SPR1 at Ser6, which promotes the disassociation of SPR1 from microtubules and facilitates microtubule disassembly. Compared with the wild type, the *spr1* mutant exhibited significantly greater water loss and reduced ABA responses, including stomatal closure and microtubule disassembly in guard cells. These phenotypes were restored by introducing the phosphorylated active form of SPR1. Our findings demonstrate that SPR1 positively regulates microtubule disassembly during ABA-induced stomatal closure, which depends on OST1-mediated phosphorylation. These findings reveal a specific connection between a core component of ABA signaling and MAPs.

Introduction

Stomata are small pores surrounded by a pair of specialized guard cells on the surface of leaves and stems, and these pores allow land plants to maintain homeostasis by enabling gas exchange with the environment, including the uptake of carbon dioxide for photosynthesis and the loss of water vapor through transpiration (Blatt, 2000; Hetherington and Woodward, 2003). Guard cells have developed sophisticated mechanisms to sense and rapidly respond to diverse environmental and stress signals, such as light, temperature, and drought. Changes in cell morphology control stomatal behavior, promoting the opening or closing of stomatal pores. Among these signals, the phytohormone abscisic acid (ABA), which is triggered by drought stress, promotes

Received April 25, 2022. Accepted September 15, 2022. Advance access publication October 18, 2022

附录

RESEARCH ARTICLE

HY5 inhibits lateral root initiation in Arabidopsis through negative regulation of the microtubule-stabilizing protein TPXL5

Yanmin Qian[1], Xiaohong Wang[1], Yimin Liu, Xiangfeng Wang*, and Tonglin Mao*

State Key Laboratory of Plant Physiology and Biochemistry; Department of Plant Sciences, College of Biological Sciences, China Agricultural University, Beijing 100193, China

[1] These authors contributed equally to this work.

*Correspondence to: **Xiangfeng Wang** (wangxf2017@cau.edu.cn) and **Tonglin Mao** (maotl2005@cau.edu.cn)

Short title: TPXL5 in lateral root initiation

One-sentence summary: The microtubule-stabilizing protein TPXL5 regulates microtubule reorganization and cell remodeling during lateral root initiation mediated by the transcription factor HY5.

The author responsible for the distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plcell/) are Xiangfeng Wang (wangxf2017@cau.edu.cn) and Tonglin Mao (maotl2005@cau.edu.cn).

ABSTRACT

Tight control of lateral root (LR) initiation is vital for root system architecture and function. Regulation of cortical microtubule reorganization is involved in the asymmetric radial expansion of founder cells during LR initiation in Arabidopsis (*Arabidopsis thaliana*). However, critical genetic evidence on the role of microtubules in LR initiation is lacking and the mechanisms underlying this regulation are poorly understood. Here, we found that the previously uncharacterized microtubule-stabilizing protein TPX2-LIKE5 (TPXL5) participates in LR initiation, which is finely regulated by the transcription factor ELONGATED HYPOCOTYL5 (HY5). In *tpxl5* mutants, LR density was decreased and more LR primordia (LRPs) remained in stage I, indicating delayed LR initiation. In particular, the cell width in the peripheral domain of LR founder cells after the first asymmetric cell division was larger in *tpxl5* mutants than in the wild type. Consistently, ordered transverse cortical microtubule arrays were not well generated in *tpxl5* mutants. In addition, HY5 directly targeted the promoter of *TPXL5* and downregulated *TPXL5* expression. The *hy5* mutant exhibited higher LR density and fewer stage I LRPs, indicating accelerated LR initiation. Such phenotypes were partially suppressed by *TPXL5* knockout. Taken together, our data provide genetic evidence supporting the notion that cortical microtubules are essential for LR initiation and unravel a molecular mechanism underlying HY5 regulation of TPXL5-mediated microtubule

附录

10. Pereira, J., Ribeiro, M.C., Battiston, F., and Jordan, F. (2022). Reconstruction and variability of tropical pollination networks in the Brazilian Atlantic Forest. Community Ecol. *23*, 315–325.

11. Rabelo, R.S., Dyer, L.A., Lepesqueur, C., Salcido, D.M., da Silva, T.P., Rodrigues, H.P.A., Trindade, T.B., Diniz, I.R., Nascimento, A.R., Tepe, E.J., and Massad, T.J. (2021). Tritrophic interaction diversity in gallery forests: A biologically rich and understudied component of the Brazilian cerrado. Arthro. Plant Interact. *15*, 773–785.

12. Villar, N., Paz, C., Zipparro, V., Nazareth, S., Bulascoschi, L., Bakker, E.S., and Galetti, M. (2021). Frugivory underpins the nitrogen cycle. Funct. Ecol. *35*, 357–368.

13. Beard, K.H., Vogt, K.A., and Kulmatiski, A. (2002). Top-down effects of a terrestrial frog on forest nutrient dynamics. Oecologia *133*, 583–593.

Plant genetics: Mechanisms of wild soybean adaptation

Yameng Liang[1] and Feng Tian[1,2,*]
[1]State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center, Center for Crop Functional Genomics and Molecular Breeding, Key Laboratory of Biology and Genetic Improvement of Maize (MOA), Beijing Key Laboratory of Crop Genetic Improvement, China Agricultural University, Beijing, China
[2]Sanya Institute of China Agricultural University, Hainan, China
*Correspondence: ft55@cau.edu.cn
https://doi.org/10.1016/j.cub.2022.12.009

A new study shows that natural variation in the flowering repressor *E1-like-a* (*Tof4*/*E1La*) promoted wild soybean adaptation to high latitudes. This lost early-flowering allele can be reintroduced into cultivated soybean for developing early-maturing cultivars.

Cultivated soybean (*Glycine max*) was domesticated from its wild progenitor (*Glycine soja*) around 5000 years ago in the temperate regions between 32–40°N in China[1,2]. Wild soybean is a facultative short-day plant and is highly sensitive to photoperiods — it will flower earlier under short day conditions, and will flower later under long day conditions. During soybean domestication and improvement, photoperiod-insensitive alleles were selected by humans, allowing soybean to be grown over a wide range of latitudes, from 53°N to 35°S. In parallel, wild soybean also spread into a broad geographic region from 24°N to 53°N, driven by natural selection. Two critical evolutionary questions thus come up: how did wild and cultivated soybean independently adapt into high and low latitudes? Do they share similar molecular and evolutionary mechanisms of adaptation? A series of genes that contributed to cultivated soybean adaptation to different latitudes have been identified[3–10]. However, how wild soybean adapted to wide latitudinal regions remains poorly understood. In this issue of *Current Biology*, Dong *et al.*[11] elegantly discovered that natural variants in *Timing of flowering 4* (*Tof4*) locus were naturally selected to promote wild soybean adaptation to high latitudes. This paper, together with a recent study from the same group[6], provides critical insights into the genetic mechanisms of the adaptation of wild soybean to high latitudes and also helps understand how the same trait like flowering time would evolve if driven by natural selection and artificial selection, respectively.

Flowering is a milestone in the process of plant development, indicating a switch from vegetative to reproductive growth. The time of flowering is regulated by a combination of exogenous and endogenous cues. Photoperiod is one of the most important environmental factors that affects the flowering time of plants. In the model species *Arabidopsis*, *CONSTANS* (*CO*) plays a central role in mediating photoperiodic flowering[12]. However, the legume-specific B3-like transcription factor E1 appears to act as a core hub in photoperiod regulation in soybean. E1 integrates the signals from photoreceptors (E3/phyA3 and E4/phyA2) and circadian clocks (J/ELF3, LUX1, LUX2, Tof16/LHY1a, Tof11/PRR3a and Tof12/PRR3b) to regulate the expression of florigen genes (*FT2a* and *FT5a*) and *Tof5*/*FUL2a* to modulate soybean photoperiodic flowering (Figure 1A)[3–5,9,13,14]. It is important to note that a recent study[9] from the same group revealed that phyAs not only regulates *E1* transcriptional level by interacting with and degrading LUXs protein to relieve the repression of evening complex (ELF4–ELF3–LUX) on *E1*, but also regulates *E1* posttranscriptional level by directly associating with E1 protein to regulate its stability. The natural variation in this *E1*-centered photoperiodic flowering network provided the genetic basis for wild and cultivated soybean adaptation to wide ecological zones.

To identify genes conferring the adaptation of wild soybean to high latitudes, Dong *et al.*[11] performed a genome-wide association study (GWAS) for flowering time in 295 diverse wild soybean accessions grown in natural long day conditions. *Tof4*, a quantitative trait locus on chromosome 4, was found to be significantly associated with flowering time. Further fine mapping using a near isogenic line population derived from the cross between Dongnong50 (DN50, a

Plant Biotechnology Journal Open Access

附录

Plant Biotechnology Journal (2022), pp. 1–12 doi: 10.1111/pbi.13927

A teosinte-derived allele of an HKT1 family sodium transporter improves salt tolerance in maize

Ming Zhang[1,2,†], Yidan Li[3,†], Xiaoyan Liang[1], Minhui Lu[2], Jinsheng Lai[2,4], Weibin Song[2,4] and Caifu Jiang[1,2,*]

[1]*State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing, China*

[2]*Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing, China*

[3]*Agro-Biotechnology Research Institute, Jilin Academy of Agricultural Sciences, Changchun, China*

[4]*Laboratory of Agrobiotechnology and National Maize Improvement Center of China, Department of Agronomy and Biotechnology, China Agricultural University, Beijing, China*

Received 18 May 2022;
accepted 11 September 2022.
**Correspondence* (Tel +86 10-62732331; fax +86 10-62732331; email cfjiang@cau.edu.cn)
[†]These authors contributed equally to this study.

Keywords: maize, salt tolerance, Na^+ transport, Na^+ transporter.

Summary

The sodium cation (Na^+) is the predominant cation with deleterious effects on crops in salt-affected agricultural areas. Salt tolerance of crop can be improved by increasing shoot Na^+ exclusion. Therefore, it is crucial to identify and use genetic variants of various crops that promote shoot Na^+ exclusion. Here, we show that a HKT1 family gene *ZmNC3* (*Zea mays* L. *Na^+ Content 3*; designated *ZmHKT1;2*) confers natural variability in shoot-Na^+ accumulation and salt tolerance in maize. *ZmHKT1;2* encodes a Na^+-preferential transporter localized in the plasma membrane, which mediates shoot Na^+ exclusion, likely by withdrawing Na^+ from the root xylem flow. A naturally occurring nonsynonymous SNP (SNP947-G) increases the Na^+ transport activity of ZmHKT1;2, promoting shoot Na^+ exclusion and salt tolerance in maize. SNP947-G first occurred in the wild grass teosinte (at a allele frequency of 43%) and has become a minor allele in the maize population (allele frequency 6.1%), suggesting that SNP947-G is derived from teosinte and that the genomic region flanking SNP947 likely has undergone selection during domestication or post-domestication dispersal of maize. Moreover, we demonstrate that introgression of the SNP947-G *ZmHKT1;2* allele into elite maize germplasms reduces shoot Na^+ content by up to 80% and promotes salt tolerance. Taken together, *ZmNC3/ZmHKT1;2* was identified as an important QTL promoting shoot Na^+ exclusion, and its favourable allele provides an effective tool for developing salt-tolerant maize varieties.

Introduction

Crops in agricultural environments are exposed to various biotic and abiotic stressors (Munns *et al*., 2012; Zhu, 2016). Salt stress is a widespread form of environmental stress that limits global crop production and agricultural sustainability (Ismail and Horie, 2017; van Zelm *et al*., 2020; Yu *et al*., 2020), and the area of salinized farmland is continuously increasing as a result of extreme climate events (e.g., drought), irrational irrigation and other factors (Hanks *et al*., 1978; Munns and Tester, 2008). To address the deleterious impact of salt stress on global agriculture, it is important to identify new salt-tolerant genes/alleles and to develop crops with improved salt tolerance (Flowers, 2004; Munns and Tester, 2008).

Previous studies have demonstrated that salt stress damages plants largely by causing osmotic stress and ion (mainly sodium ion; Na^+) toxicity (Munns and Tester, 2008; Geilfus *et al*., 2018; Gong *et al*., 2020; Steinhorst and Kudla, 2019). In order to adapt to saline environments, plants have evolved complex networks that, respectively, regulate the osmotic and ionic aspects of salt tolerance (Munns and Tester, 2008; Zhang *et al*., 2018), one of which is to utilize Na^+-preferential transporters to circulate Na^+, thus protecting plants from damage caused by excessive Na^+ accumulation (Greenway and Munns, 1980; Horie *et al*., 2009; Zhang *et al*., 2018; Yang & Guo, 2018a, 2018b; Zhu, 2016). For example, the Arabidopsis Na^+/H^+ transporter SOS1 mediates the root-to-rhizosphere efflux of Na^+ (Shi *et al*., 2003; Zhu, 2016); the Na^+/H^+ EXCHANGER antiporters AtNHX1 likely mediates sequestration of Na^+ into vacuole (Munns and Tester, 2008); the maize HAK family transporter ZmHAK4 mediates unloading of xylem Na^+ (Zhang *et al*., 2019) and the High-affinity K^+ Transporter (HKT) family transporters (e.g., AtHKT1;1) mediate Na^+ exclusion from shoots and flowers (An *et al*., 2017; Busomes *et al*., 2018; Horie *et al*., 2009). These Na^+ transporters and their regulators act together to modulate Na^+ homeostasis at the cellular, tissue and organismic levels, thereby improving tolerance to salt stress (Brownlee, 2018; Chu *et al*., 2021; Munns and Tester, 2008).

Members of the HKT transporter family are among the most-studied plant transporter proteins and can be classified into two subfamilies: class 1 (HKT1) and class 2 (HKT2) (Horie *et al*., 2009; Schachtman and Schroeder, 1994). Ion-transport selectivity of HKT family transporters is associated with a conservative residue in the first pore loop, in which a serine (HKT1 members) is closely associated with Na^+ preference and a glycine (HKT2) is associated with K^+ permeability as well as Na^+ permeability, with some

Please cite this article as: Zhang, M., Li, Y., Liang, X., Lu, M., Lai, J., Song, W. and Jiang, C. (2022) A teosinte-derived allele of an HKT1 family sodium transporter improves salt tolerance in maize. *Plant Biotechnol J*., https://doi.org/10.1111/pbi.13927.

附录

Yang et al. Journal of Nanobiotechnology (2022) 20:219
https://doi.org/10.1186/s12951-022-01443-4

Journal of Nanobiotechnology

RESEARCH Open Access

Construction and application of star polycation nanocarrier-based microRNA delivery system in *Arabidopsis* and maize

Jia Yang[1†], Shuo Yan[2†], Shipeng Xie[1], Meizhen Yin[3], Jie Shen[2], Zhaohu Li[1], Yuyi Zhou[1*] and Liusheng Duan[1,4*]

Abstract

Background: MicroRNA (miRNA) plays vital roles in the regulation of both plant architecture and stress resistance through cleavage or translation inhibition of the target messenger RNAs (mRNAs). However, miRNA-induced gene silencing remains a major challenge in vivo due to the low delivery efficiency and instability of miRNA, thus an efficient and simple method is urgently needed for miRNA transformation. Previous researches have constructed a star polycation (SPc)-mediated transdermal double-stranded RNA (dsRNA) delivery system, achieving efficient dsRNA delivery and gene silencing in insect pests.

Results: Here, we tested SPc-based platform for direct delivery of double-stranded precursor miRNA (ds-*MIRNA*) into protoplasts and plants. The results showed that SPc could assemble with ds-*MIRNA* through electrostatic interaction to form nano-sized ds-*MIRNA*/SPc complex. The complex could penetrate the root cortex and be systematically transported through the vascular tissue in seedlings of *Arabidopsis* and maize. Meanwhile, the complex could up-regulate the expression of endocytosis-related genes in both protoplasts and plants to promote the cellular uptake. Furthermore, the SPc-delivered ds-*MIRNA* could efficiently increase mature miRNA amount to suppress the target gene expression, and the similar phenotypes of *Arabidopsis* and maize were observed compared to the transgenic plants overexpressing miRNA.

Conclusion: To our knowledge, we report the first construction and application of star polycation nanocarrier-based platform for miRNA delivery in plants, which explores a new enable approach of plant biotechnology with efficient transformation for agricultural application.

Keywords: Gene silencing, MiRNA delivery, Nanoparticle, Plant biotechnology, Star polycation

[†]Jia Yang and Shuo Yan have contributed equally to this work

*Correspondence: zhouyuyi@cau.edu.cn; duanlsh@cau.edu.cn

[1] State Key Laboratory of Plant Physiology and Biochemistry, Engineering Research Center of Plant Growth Regulator, Ministry of Education & College of Agronomy and Biotechnology, China Agricultural University, No. 2 Yuanmingyuan West Road, Haidian District, Beijing 100193, People's Republic of China
Full list of author information is available at the end of the article

附录

Journal of Cleaner Production 331 (2022) 129964

Contents lists available at ScienceDirect

Journal of Cleaner Production

journal homepage: www.elsevier.com/locate/jclepro

Optimizing nitrogen management diminished reactive nitrogen loss and acquired optimal net ecosystem economic benefit in a wheat-maize rotation system

Churong Liu [a], Danyang Ren [a], Hongrun Liu [a], Yushi Zhang [a], Ligang Wang [b], Zhaohu Li [a], Mingcai Zhang [a,*]

[a] State Key Laboratory of Plant Physiology and Biochemistry, Engineering Research Center of Plant Growth Regulator, Ministry of Education, College of Agronomy and Biotechnology, China Agricultural University, Beijing, 100193, China
[b] Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, China

ARTICLE INFO

Handling Editor: Bin Chen

Keywords:
Reactive nitrogen loss
Nitrification inhibitor
Urease inhibitor
Nr damage cost
Net economic benefits
Optimizing nitrogen management

ABSTRACT

Excessive nitrogen (N) application results in substantial losses, as N fertilizers are wasted along with the loss of reactive N (Nr), thereby posing substantial threats to both human and ecosystem health. Nitrification inhibitors (NI) and urease inhibitors (UI) have the potential to reduce Nr loss as well as improve grain yields. However, comprehensive benefit assessments of these inhibitors from an environmental and economic perspective, including insights into the mechanisms of N fertilizer reduction, are lacking. Conducting a two-year study of a wheat-maize rotation system, urea (Ur), NI, UI, and joint inhibitors (UI + NI, UN) was established at three N rates (N1: suboptimal rate, N2: recommended rate, and N3: farmers' rate), including a N fertilizer-lacking site (N0) as a control. N fertilizer increment stimulated foreground Nr loss, and increased field Nr loss through NH_3 volatilization, N_2O emissions, and NO_3^- leaching. There was seasonal variation in the Nr loss pathway between the maize and wheat seasons, and NO_3^- leaching only occurred during the maize season. Compared with farmers' N practice (N3Ur), N reduction and inhibitor application decreased field Nr losses by 10.9–85.2%. The efficiency of inhibitors also varied seasonally, and UI exhibited higher efficiency in the wheat season while UN in the maize season. N reduction and inhibitor application decreased the NDC by 18.4–83.1%, where N1UN and N1UI exhibited higher efficiency. Compared with N3Ur, N1Ur had a risk of yield reduction (7.6–13.9%), with N1UN and N1UI exhibiting no significant difference. The use of suitable inhibitors effectively compensated for the increase in NDC and reduction in yield under the N1 rate. Moreover, N1UN obtained the highest net economic benefits (NEB) in the maize season while N1UI in the wheat season. The combination of N1UN for maize season and N1UI for wheat season as optimizing N management, which improved the NEB by 24.7% on average compared with the farmers' N practice in the wheat-maize rotation. This optimizing N management for minimal environmental damage and maximum economic benefits could be conducive for sustainable, intensive wheat-maize cropping systems in the North China Plain.

1. Introduction

Nitrogen (N) being an indispensable nutrient for crop growth, N fertilization can be considered an important tool to improve food security (Yu et al., 2019). N fertilizer inputs are currently ramped up owing to a rapid increase in food demand, which consequentially increases the substantial reactive N (Nr) losses into the environment (Zhang et al., 2015; Guo et al., 2020; FAO, 2021). Over-fertilization also occurs in the North China Plain (NCP), an important winter wheat-summer maize rotation region, contributing one-fourth of the total grain production in the intensive agricultural area of China (Sun et al., 2010). In NCP, to meet the food requirement, 300–350 kg N ha^{-1} $season^{-1}$ or even higher N fertilizer is applied by farmers, contributing to the loss of approximately a quarter of the Nr in this region (Cui et al., 2009; Ju et al., 2009; Zhang et al., 2019). The main field Nr losses, including gaseous discharge as NH_3 volatilization and N_2O emission, contribute significantly to air pollution and climate change (Ravinshakara et al., 2009; Benbi, 2013; Gong et al., 2013; Duan et al., 2019),

* Corresponding author.
E-mail address: zmc1214@163.com (M. Zhang).

https://doi.org/10.1016/j.jclepro.2021.129964
Received 24 June 2021; Received in revised form 22 November 2021; Accepted 29 November 2021
Available online 1 December 2021

ECAP is a key negative regulator mediating different pathways to modulate salt stress-induced anthocyanin biosynthesis in Arabidopsis

Changjiang Li* , Lei Shi* , Xing Li* , Yanan Wang , Yujing Bi , Wei Li , Huifang Ma , Binqing Chen , Lei Zhu and Ying Fu

State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China

Author for correspondence:
Ying Fu
Email: yingfu@cau.edu.cn

Received: 20 September 2021
Accepted: 13 December 2021

New Phytologist (2022) 233: 2216–2231
doi: 10.1111/nph.17937

Key words: anthocyanin, Arabidopsis thaliana, ECAP, high salinity, jasmonate signaling, MYB75/PAP1.

Summary

- Anthocyanins are a subgroup of plant flavonoids with antioxidant activities and are often induced by various biotic and abiotic stresses in plants, probably to efficiently scavenge free radicals and reactive oxygen species. However, the regulatory mechanisms of salt stress-induced anthocyanin biosynthesis remain unclear.
- Using molecular and genetic techniques we demonstrated key roles of ECAP in differential salt-responsive anthocyanin biosynthesis pathways in Arabidopsis thaliana.
- ECAP, JAZ6/8 and TPR2 are known to form a transcriptional repressor complex, and negatively regulate jasmonate (JA)-responsive anthocyanin accumulation. In this study, we demonstrated that under moderate salt stress, the accumulation of anthocyanins is partially dependent on JA signaling, which degrades JAZ proteins but not ECAP. More interestingly, we found that high salinity rather than moderate salinity induces the degradation of ECAP through the 26S proteasome pathway, and this process is independent of JA signaling. Further analysis revealed that ECAP interacts with MYB75 (a transcription factor activating anthocyanin biosynthetic genes) and represses its transcriptional activity in the absence of high salinity.
- Our results indicated that plants adopt different strategies for fine-tuning anthocyanin accumulation under different levels of salt stress, and further elucidated the complex regulation of anthocyanin biosynthesis during plant development and responses to environmental stresses.

Introduction

Anthocyanins are a group of plant flavonoids possessing antioxidant properties and color features, and play diverse biological functions, such as attracting pollinators and seed distributors, and resistance to pathogen attacks and environmental stresses (Wang et al., 1997; Mouradov & Spangenberg, 2014; Kovinich et al., 2015). In Arabidopsis, the anthocyanin biosynthesis pathway has been largely deciphered. The structural genes involved are usually grouped into early (such as CHS, CHI and F3H) or late biosynthetic genes (LBGs) (such as DFR, LDOX and UF3GT) (Shin et al., 2013; Xu et al., 2014). It has been demonstrated that transcription factors (TFs) from the R2R3-MYB, basic–helix–loop-helix (bHLH) and WD40 families form the ternary MBW complex to modulate the expression of structural anthocyanin biosynthetic genes (Xu et al., 2015). Several signaling pathways (such as light, jasmonate (JA) and gibberellic acid (GA) signaling) regulate anthocyanin biosynthesis via interaction with the MBW complex (Qi et al., 2011; Li et al., 2016; Xie et al., 2016).

In the MBW complex, MYBs are considered the major determinant regulators (Zimmermann et al., 2004; Baudry et al., 2006; Gonzalez et al., 2008; Bhargava et al., 2013; Lai et al., 2014; Jin et al., 2016). Arabidopsis MYB75, also known as PRODUCTION OF ANTHOCYANIN PIGMENT 1 (PAP1), is an R2R3 MYB transcription factor, and the myb75-c loss-of-function mutant has less anthocyanin content compared to the wild-type, whereas the PAP1-Dominant (pap1-D) gain-of-function mutant has greater anthocyanin accumulation (Borevitz et al., 2000; Li et al., 2016). The MBW complex composed of MYB75, bHLH TFs (EGL3, GL1, GL3 and TT8) and WD-40 protein TTG1 has been identified as an activator of anthocyanin biosynthesis via promotion of the expression of late biosynthetic genes, such as DFR, UF3GT and ANS (Gonzalez et al., 2008; Das et al., 2012; Shin et al., 2013; Xu et al., 2014; Lacchini & Goossens, 2020).

Salt stress is one of the major environmental stresses that plants suffer, and plants rely on multiple pathways, such as the salt

*These authors contributed equally to this work.

New Phytologist

附录

Research

The classical SOS pathway confers natural variation of salt tolerance in maize

Xueyan Zhou[1]*, Jianfang Li[1]*, Yiqiao Wang[1], Xiaoyan Liang[1], Ming Zhang[1], Minhui Lu[2], Yan Guo[1,2], Feng Qin[1,2] and Caifu Jiang[1,2]

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100094, China; [2]Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100094, China

Author for correspondence:
Caifu Jiang
Email: cfjiang@cau.edu.cn

Received: *20 January 2022*
Accepted: *19 May 2022*

New Phytologist (2022)
doi: 10.1111/nph.18278

Key words: maize, Na^+ regulation, natural variation, salt tolerance, SOS pathway.

Summary

- Sodium (Na^+) is the major cation damaging crops in the salinised farmland. Previous studies have shown that the Salt Overly Sensitive (SOS) pathway is important for salt tolerance in Arabidopsis. Nevertheless, the SOS pathway remains poorly investigated in most crops.
- This study addresses the function of the SOS pathway and its association with the natural variation of salt tolerance in maize.
- Firstly, we showed that a naturally occurring 4-bp frame-shifting deletion in *ZmSOS1* caused the salt hypersensitive phenotype of the maize inbred line LH65. Accordingly, mutants lacking ZmSOS1 also displayed a salt hypersensitive phenotype, due to an impaired root-to-rhizosphere Na^+ efflux and an increased shoot Na^+ concentration. We next showed that the maize SOS3/SOS2 complex (ZmCBL4/ZmCIPK24a and ZmCBL8/ZmCIPK24a) phosphorylates ZmSOS1 therefore activating its Na^+-transporting activity, with their loss-of-function mutants displaying salt hypersensitive phenotypes. Moreover, we observed that a LTR/Gypsy insertion decreased the expression of *ZmCBL8*, thereby increasing shoot Na^+ concentration in natural maize population.
- Taken together, our study demonstrated that the maize SOS pathway confers a conservative salt-tolerant role, and the components of SOS pathway (ZmSOS1 and ZmCBL8) confer the natural variations of Na^+ regulation and salt tolerance in maize, therefore providing important gene targets for breeding salt-tolerant maize.

Introduction

Soil salinity is one of the major environmental abiotic stresses that affects more than 6% (800 million hectares) of the world's land area, including *c.* 80 million hectares of land farmed by dryland or irrigation-dependent agriculture (Munns & Tester, 2008). Worryingly, the area of salt-affected land is continuing to increase due to global climate change, land clearing, as well as excessive irrigation (Flowers, 2004; Munns & Tester, 2008; Zhu, 2016), instigating soil salinity to be a growing threat to the global agriculture (Ismail & Horie, 2017). To deal with the deleterious effect of soil salinity, there is an urgent need to investigate the salt-tolerant mechanisms of crop species, therefore to facilitate the breeding of salt-tolerant crops (Ismail & Horie, 2017). Decades of effort have partially explained the complexity of crop salt tolerance, which is composed of, but not limited to the tolerance to ion (mainly Na^+ and Cl^-) toxicity and osmotic stress, the maintenance of H^+ gradient across the plasma membrane, and the tolerance to salt-induced oxidative stress (reviewed by Munns & Tester, 2008; Zhu, 2016; Li *et al.*, 2017; Yang & Guo, 2018).

Previous studies have indicated that the natural genetic diversities within cultivated crops and their wild relatives provide valuable sources for breeding salt-tolerant crops (Campbell *et al.*, 2017; Ismail & Horie, 2017; Luo *et al.*, 2019; Zhang *et al.*, 2019; Wang *et al.*, 2020). In addition, dozens of QTL genes associated with the natural variations of salt tolerance have been identified in a variety of crop species, and some of them showed great potential for application (Li, 2020; Cao *et al.*, 2021; Singh *et al.*, 2021). For instance, the gene locus *Nax2* (*Na^+ Exclusion 2*) from the wheat relative *Triticum monococcum* increases the grain yield of durum wheat by 25% under salt conditions (Byrt *et al.*, 2007; Munns *et al.*, 2012); the *SKC1* (*Shoot K^+ Content 1*) from the salt-tolerant rice variety (*Nona Bokra*) promotes salt tolerance by regulating K^+/Na^+ homeostasis (Ren *et al.*, 2005); the favourable alleles of a HAK family sodium transporter gene *ZmNC2* (*Na^+ content 2*) reduces the shoot Na^+ content of the salt-grown maize seedling by 50% (Zhang *et al.*, 2019). Although these studies have, to some extent, advanced our understanding of the natural diversities of crop salt

*These authors contributed equally to this work.

New Phytologist

附录

Research

A competition-attenuation mechanism modulates thermoresponsive growth at warm temperatures in plants

Wei Li[1,2], Ying-Ying Tian[1], Jin-Yu Li[1], Li Yuan[3], Lin-Lin Zhang[1], Zhi-Ye Wang[1], Xiaodong Xu[3], Seth Jon Davis[3,4] and Jian-Xiang Liu[1]

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Life Sciences, Zhejiang University, Hangzhou 310027, China; [2]College of Environmental and Resource Sciences, Zhejiang University, Hangzhou 310027, China; [3]State Key Laboratory of Crop Stress Adaptation and Improvement, School of Life Sciences, Henan University, Kaifeng 475004, China; [4]Department of Biology, University of York, Heslington, York, YO10 5DD, UK

Author for correspondence:
Jian-Xiang Liu
Email: jianxiangliu@zju.edu.cn

Received: *18 June 2022*
Accepted: *9 August 2022*

New Phytologist (2023) **237:** 177–191
doi: 10.1111/nph.18442

Key words: *Arabidopsis thaliana*, hypocotyl growth, RVE5, thermomorphogenesis, warm temperature.

Summary

- Global warming has profound impact on growth and development, and plants constantly adjust their internal circadian clock to cope with external environment. However, how clock-associated genes fine-tune thermoresponsive growth in plants is little understood.
- We found that loss-of-function mutation of *REVEILLE5* (*RVE5*) reduces the expression of circadian gene *EARLY FLOWERING 4* (*ELF4*) in *Arabidopsis*, and confers accelerated hypocotyl growth under warm-temperature conditions.
- Both RVE5 and CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) accumulate at warm temperatures and bind to the same EE *cis*-element presented on *ELF4* promoter, but the transcriptional repression activity of RVE5 is weaker than that of CCA1. The binding of CCA1 to *ELF4* promoter is enhanced in the *rve5-2* mutant at warm temperatures, and overexpression of *ELF4* in the *rve5-2* mutant background suppresses the *rve5-2* mutant phenotype at warm temperatures.
- Therefore, the transcriptional repressor RVE5 finetunes *ELF4* expression via competing at a *cis*-element with the stronger transcriptional repressor CCA1 at warm temperatures. Such a competition–attenuation mechanism provides a balancing system for modulating the level of ELF4 and thermoresponsive hypocotyl growth under warm-temperature conditions.

Introduction

Plants have evolved an internal timing keeping-mechanism known as the circadian clock that enables anticipation of external environmental cues to adjust growth and development (Huang & Nusinow, 2016). This clock consists of the input and output pathways, and the central oscillator (Creux & Harmer, 2019). Ambient light and temperature cues are two major inputting signals that function at both transcriptional and post-translational levels to set (entrain) this clock (Hsu & Harmer, 2014). The central oscillator at ambient temperature contains multiple repressors and activators that form interconnected feedback loops (Nagel & Kay, 2012). Briefly, the morning expressed CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY) repress the expression of daytime genes *PSEUDO-RESPONSE REGULATOR 5/7/9* (*PRR5/7/9*) and the evening gene *PRR1*/*TIMING OF CAB EXPRESSION1* (*TOC1*); in turn, the latter encoded proteins inhibit the expression of former genes *CCA1*/*LHY* (Alabadi *et al.*, 2001; Kamioka *et al.*, 2016). CCA1/LHY also inhibit the expression of evening genes of the evening complex (EC); and EC represses the expression of PRRs (Herrero *et al.*, 2012; Mizuno *et al.*, 2014). In addition, midday-expressed REVEILLE 4/6/8 (RVE4/6/8) activate the expression of *TOC1*, *PRR5* and *EC* genes, but *RVE8* expression is inhibited by TOC1 and other PRRs (Rawat *et al.*, 2011; Hsu *et al.*, 2013; Hsu & Harmer, 2014). Further, GIGANTEA (GI) promotes the expression of *CCA1*/*LHY* whereas CCA1/LHY inhibits the expression of *GI* and *TOC1* (Fowler *et al.*, 1999; Mizoguchi *et al.*, 2002). These multiple feedback loops provide rhythmic robustness across dynamic environmental conditions (Shalit-Kaneh *et al.*, 2018). It is worthy of note that the majority of gene products in the circadian clock acts as repressors, with the exception of RVE4/6/8 in the RVE8 clade which act as activators (Hsu & Harmer, 2014). As output pathways, the circadian clock regulates diurnal hypocotyl growth and photoperiod-dependent flowering (Farre, 2012).

Global warming has world-wide impacts on plant distribution and crop productivity (Lesk *et al.*, 2016). The plant circadian clock also controls hypocotyl growth under warm-temperature conditions, in a process termed thermomorphogenesis, in which plants sense and adapt to ambient warm temperatures (Park *et al.*, 2021). Several proteins/RNAs have been proposed to be warm-temperature sensors in plants. For example, phytochrome B (phyB), originally characterized as a photoreceptor (Lin *et al.*, 2020), is a temperature sensor. Warm temperature accelerates the conversion of phyB from active Pfr to inactive Pr, which reduces

New Phytologist

附录

Research

14-3-3 proteins regulate photomorphogenesis by facilitating light-induced degradation of PIF3

Pengyu Song[1]*, Zidan Yang[1,2]*, Can Guo[1], Run Han[1], Huaichang Wang[1], Jie Dong[3], Dingming Kang[2], Yan Guo[1], Shuhua Yang[1] and Jigang Li[1]

[1]State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China; [2]MOE Key Laboratory of Crop Heterosis and Utilization, College of Agronomy and Biotechnology, China Agricultural University, Beijing 100193, China; [3]Institute of Crop Science, Zhejiang University, Hangzhou 310058, China

Author for correspondence:
Jigang Li
Email: jigangli@cau.edu.cn

Received: *28 July 2022*
Accepted: *9 September 2022*

New Phytologist (2022)
doi: 10.1111/nph.18494

Key words: 14-3-3, Arabidopsis, photomorphogenesis, phytochrome, PIF3.

Summary

- 14-3-3s are highly conserved phosphopeptide-binding proteins that play important roles in various developmental and signaling pathways in plants. However, although protein phosphorylation has been proven to be a key mechanism for regulating many pivotal components of the light signaling pathway, the role of 14-3-3 proteins in photomorphogenesis remains largely obscure. PHYTOCHROME-INTERACTING FACTOR3 (PIF3) is an extensively studied transcription factor repressing photomorphogenesis, and it is well-established that upon red (R) light exposure, photo-activated phytochrome B (phyB) interacts with PIF3 and induces its rapid phosphorylation and degradation. PHOTOREGULATORY PROTEIN KINASES (PPKs), a family of nuclear protein kinases, interact with phyB and PIF3 in R light and mediate multisite phosphorylation of PIF3 *in vivo*.
- Here, we report that two members of the 14-3-3 protein family, 14-3-3λ and κ, bind to a serine residue in the bHLH domain of PIF3 that can be phosphorylated by PPKs, and act as key positive regulators of R light-induced photomorphogenesis.
- Moreover, 14-3-3λ and κ preferentially interact with photo-activated phyB and promote the phyB-PIF3-PPK complex formation, thereby facilitating phyB-induced phosphorylation and degradation of PIF3 upon R light exposure.
- Together, our data demonstrate that 14-3-3λ and κ work in close concert with the phyB-PIF3 module to regulate light signaling in Arabidopsis.

Introduction

Light serves as an important environmental factor affecting almost every developmental stage of plants. Light signal is perceived by various families of photoreceptors that respond to specific wavelengths of the spectrum. However, although phytochromes (phys) are considered as the red (R) and far-red (FR) light photoreceptors in plants, they also can absorb blue (B) light, and thus play fundamental roles in mediating the adaptive responses of plants under various light conditions (Li *et al.*, 2011; Legris *et al.*, 2019; Cheng *et al.*, 2021). The Arabidopsis (*Arabidopsis thaliana*) genome encodes five phytochrome photoreceptors, named phytochrome A (phyA) to phyE (Li *et al.*, 2011). Phytochromes are classified into two types: phyA is classified as a type I photo-labile phytochrome and is responsible for mediating photomorphogenic responses in FR light, whereas phyB to phyE are classified as Type II light-stable phytochromes, and phyB plays a major role in regulating de-etiolation response in R light (Li *et al.*, 2011; Legris *et al.*, 2019; Cheng *et al.*, 2021). Phytochromes exist *in vivo* in two interconvertible forms: the R light-absorbing Pr form and the FR light-absorbing Pfr form (Bae & Choi, 2008; Li *et al.*, 2011). It has long been believed that the Pfr form is biologically active, whereas the Pr form is inactive; however, it was recently proposed that the Pr form of phyA may have some biological activity when it is localized in the nucleus (Li & Hiltbrunner, 2021). In darkness, phytochromes are synthesized in the cytosol in the Pr form; upon light irradiation, they convert to the Pfr form and translocate into the nucleus, where they transduce the light signal by interacting with numerous signaling partners (Jiao *et al.*, 2007; Fankhauser & Chen, 2008; Franklin & Quail, 2010; Li *et al.*, 2011; Legris *et al.*, 2019).

PHYTOCHROME-INTERACTING FACTORS (PIFs) are a subfamily of basic-helix-loop-helix (bHLH) transcription factors (Khanna *et al.*, 2004; Leivar & Quail, 2011). PIFs act as negative regulators of photomorphogenesis and accumulate at high levels in darkness; however, upon light exposure, photo-activated phytochromes interact with PIFs and induce their rapid phosphorylation and degradation through the ubiquitin/26S proteasome pathway (Castillon *et al.*, 2007; Leivar & Quail, 2011). PIF3 is the foundation member of eight PIF proteins (named

*These authors contributed equally to this work.

Maize cytosolic invertase INVAN6 ensures faithful meiotic progression under heat stress

Wei Huang[1,2,3]*, Yunfei Li[1,2]*, Yan Du[1], Lingling Pan[1,2], Yumin Huang[1,2], Hongbing Liu[1,2], Yue Zhao[1,2], Yunlu Shi[2], Yong-Ling Ruan[4], Zhaobin Dong[1,2] and Weiwei Jin[1,2,3,5]

[1]State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center, Key Laboratory of Crop Heterosis and Utilization (MOE), Joint Laboratory for International Cooperation in Crop Molecular Breeding (MOE), China Agricultural University, Beijing 100193, China; [2]Center for Crop Functional Genomics and Molecular Breeding, China Agricultural University, Beijing 100193, China; [3]Sanya Institute of China Agricultural University, Sanya 572025, China; [4]Division of Plant Sciences, Research School of Biology, The Australian National University, Canberra ACT 2601, Australia; [5]Fresh Corn Research Center of BTH, College of Agronomy & Resources and Environment, Tianjin Agricultural University, Tianjin 300384, China

Authors for correspondence:
Zhaobin Dong
Email: zbdong@cau.edu.cn

Weiwei Jin
Email: weiweijin@cau.edu.cn

Received: *28 April 2022*
Accepted: *25 August 2022*

New Phytologist (2022) **236:** 2172–2188
doi: 10.1111/nph.18490

Key words: cytosolic invertase, heat stress, male sterility, meiosis, *Zea mays*.

Summary

- Faithful meiotic progression ensures the generation of viable gametes. Studies suggested the male meiosis of plants is sensitive to ambient temperature, but the underlying molecular mechanisms remain elusive.
- Here, we characterized a maize (*Zea mays* ssp. *mays* L.) dominant male sterile mutant *Mei025*, in which the meiotic process of pollen mother cells (PMCs) was arrested after pachytene.
- An Asp-to-Asn replacement at position 276 of INVERTASE ALKALINE NEUTRAL 6 (INVAN6), a cytosolic invertase (CIN) that predominantly exists in PMCs and specifically hydrolyses sucrose, was revealed to cause meiotic defects in *Mei025*. INVAN6 interacts with itself as well as with four other CINs and seven 14-3-3 proteins. Although INVAN6^{Mei025}, the variant of INVAN6 found in *Mei025*, lacks hydrolytic activity entirely, its presence is deleterious to male meiosis, possibly in a dominant negative repression manner through interacting with its partner proteins. Notably, heat stress aggravated meiotic defects in *invan6* null mutant. Further transcriptome data suggest INVAN6 has a fundamental role for sugar homeostasis and stress tolerance of male meiocytes.
- In summary, this work uncovered the function of maize CIN in male meiosis and revealed the role of CIN-mediated sugar metabolism and signalling in meiotic progression under heat stress.

Introduction

Meiosis, a specialized cell division in eukaryotes, generates haploid gametes with a halved number of chromosome sets through two rounds of chromosome segregation following a single round of DNA replication. During prophase I, meiotic chromosomes are packaged from long, thin threads into short, fatter entities, in coordination with the pairing, synapsis, and recombination of homologous chromosomes (Hamant *et al.*, 2006; Mercier *et al.*, 2015). The dynamic reconstruction of chromosomes ensures the faithful partitioning of homologues and cell cycle progression. In plants, male meiosis is sensitive to ambient temperature (De Storme & Geelen, 2014; Modliszewski & Copenhaver, 2017; Liu *et al.*, 2019). Mildly decreased or increased temperature promotes meiotic recombination rate in Arabidopsis (Francis *et al.*, 2007; Lloyd *et al.*, 2018; Modliszewski *et al.*, 2018), whereas excessively high temperature inhibits double-strand breaks (DSBs) generation and compromises homologue synapsis (Ning *et al.*, 2021; Fu *et al.*, 2022). In both monocots and dicots, cold and heat stresses interfere with radial microtubule arrays and induce polyploid gametes (Tang *et al.*, 2011; De Storme *et al.*, 2012; Draeger & Moore, 2017; Wang *et al.*, 2017; Liu *et al.*, 2019; Lei *et al.*, 2020; Schindfessel *et al.*, 2021). In addition to the aberrant cytokinesis, heat stress impairs chromosome behaviours in pollen mother cells (PMCs), resulting in partial asynapsis, chromosome bridges, and micronuclei formation (Draeger & Moore, 2017; Wang *et al.*, 2017; De Storme & Geelen, 2020; Schindfessel *et al.*, 2021). Compared with the extensive recording of meiotic recombination and progression at varied temperatures, genes involved in the thermotolerance of meiosis have been rarely identified. One classical gene is *Cyclin-Dependent Kinase G1*, which regulates meiotic chromosome recombination and synapsis in a temperature-dependent manner in Arabidopsis (Zheng *et al.*, 2014; Nibau *et al.*, 2020). And a recent study in maize (*Zea mays*) revealed that Heat Shock Protein 101 is essential for DSB repair and subsequent meiosis under heat stress (Li *et al.*, 2022). To

*These authors contributed equally to this work.

附录

Science of the Total Environment 806 (2022) 151225

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Fertilizer stabilizers reduce nitrous oxide emissions from agricultural soil by targeting microbial nitrogen transformations

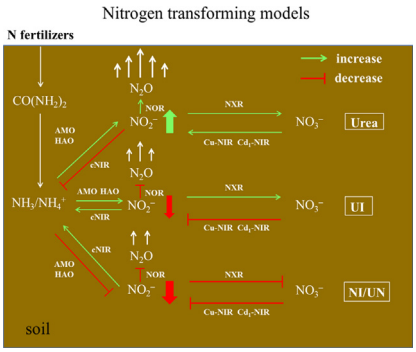
Churong Liu [a], Yushi Zhang [a], Hongrun Liu [a], Xueqing Liu [a], Danyang Ren [a], Ligang Wang [b], Dahai Guan [c], Zhaohu Li [a], Mingcai Zhang [a,*]

[a] State Key Laboratory of Plant Physiology and Biochemistry, Engineering Research Center of Plant Growth Regulator, Ministry of Education, China Agricultural University, Beijing 100193, China
[b] Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing 100081, China
[c] Rural Energy and Environment Agency, Ministry of Agriculture and Rural Affairs, Beijing 100125, China

HIGHLIGHTS

- Effects and mechanisms of N stabilizers on soil N_2O emissions were examined.
- N_2O mitigation related to low NO_2^- concentration and abundance of NO_2^- producer genes.
- Urea increased microorganisms positively correlated with N_2O emissions.
- NBPT reduced N_2O emissions by reducing denitrification genes.
- DMPP reduced N_2O emissions by reducing NH_3 oxidation and denitrification genes.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 30 July 2021
Received in revised form 21 October 2021
Accepted 21 October 2021
Available online 27 October 2021

Editor: Wei Shi

Keywords:
3,4-dimethylpyrazole phosphate (DMPP)
Functional genes
Shotgun metagenomics
N cycling
N-(n-butyl) thiophosphoric triamide (NBPT)
Soil microbial communities

ABSTRACT

Nitrous oxide (N_2O) is a pollutant released from agriculture soils following N fertilizer application. N stabilizers, such as N-(n-butyl) thiophosphoric triamide (NBPT) and 3,4-dimethylpyrazole phosphate (DMPP) could mitigate these N_2O emissions when applied with fertilizer. Here, field experiments were conducted to investigate the microbial mechanisms by which NBPT and DMPP mitigate N_2O emissions following urea application. We determined dynamic N_2O emissions and inorganic N concentrations for two wheat seasons and combined this with metagenomic sequencing. Application of NBPT, DMPP, and both NBPT and DMPP together with urea decreased mean N_2O accumulative emissions by 77.8, 91.4 and 90.7%, respectively, compared with urea application alone, mainly via repressing the increase in NO_2^- concentration after N fertilization. Sequencing results indicated that urea application enriched microorganisms that were positively correlated with N_2O production, whereas N stabilizers enriched microorganisms that were negatively correlated with N_2O production. Furthermore, compared to urea application alone, NBPT with urea reduced the abundances of genes related to denitrification, including *napA*/*nasA*, *nirS*/*nirK*, and *norBC*, resulting in a higher soil NO_3^- pool. Conversely, DMPP application, either alone or together with NBPT, decreased the abundance of genes involved in ammonia oxidation and denitrification, including *amoCAB*, *hao*, *napA*/*nasA*, *nirS*/*nirK*, and *norBC*, and maintained a greater soil NH_4^+ pool. Both N stabilizers resulted in similar abundances of *nirABD*—which is related to NO_2^- reducers—as when no N fertilizer was applied, which could prevent NO_2^- accumulation, consequently

Abbreviations: AMO, ammonia monooxygenase; AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; DMPP, 3,4-dimethylpyrazole phosphate; NBPT, N-(n-butyl) thiophosphoric triamide; NI, urea + DMPP treatment; NOB, nitrite-oxidizing bacteria; NOR, nitric oxide reductases; NOS, nitrous oxide reductase; UI, urea + NBPT treatment; UN, urea + NBPT + DMPP treatment; Urea, urea treatment; WFPS, water-filled pore space.

* Corresponding author.
E-mail addresses: zmc1214@163.com, zhangmingcai@cau.edu.cn (M. Zhang).

https://doi.org/10.1016/j.scitotenv.2021.151225

附录

Journal Pre-proofs

Database

WheatCENet: A database for comparative co-expression networks analysis of allohexaploid wheat and its progenitors

Zhongqiu Li, Yiheng Hu, Xuelian Ma, Lingling Da, Jiajie She, Yue Liu, Xin Yi, Yaxin Cao, Wenying Xu, Yuannian Jiao, Zhen Su

PII: S1672-0229(22)00071-7
DOI: https://doi.org/10.1016/j.gpb.2022.04.007
Reference: GPB 632

To appear in: *Genomics, Proteomics & Bioinformatics*

Received Date: 12 August 2021
Revised Date: 16 March 2022
Accepted Date: 8 May 2022

Please cite this article as: Z. Li, Y. Hu, X. Ma, L. Da, J. She, Y. Liu, X. Yi, Y. Cao, W. Xu, Y. Jiao, Z. Su, WheatCENet: A database for comparative co-expression networks analysis of allohexaploid wheat and its progenitors, *Genomics, Proteomics & Bioinformatics* (2022), doi: https://doi.org/10.1016/j.gpb.2022.04.007

附录

https://doi.org/10.1093/plphys/kiac233 PLANT PHYSIOLOGY 2022: 189: 1916–1919

Plant Physiology®

The transcription factor ZmMYB69 represses lignin biosynthesis by activating *ZmMYB31/42* expression in maize

Zhiquan Qiang [1], Honghua Sun,[1] Fanghui Ge [1], Wei Li [1], Changjiang Li,[1] Shuwei Wang [1], Baocai Zhang [2], Lei Zhu [1], Shuaisong Zhang [1], Xiqing Wang [1], Jinsheng Lai [3], Feng Qin [1], Yihua Zhou [2] and Ying Fu [1,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry, College of Biological Sciences, China Agricultural University, Beijing 100193, China
2 State Key Laboratory of Plant Genomics, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing 100083, China
3 State Key Laboratory of Plant Physiology and Biochemistry, National Maize Improvement Center, Department of Plant Genetics and Breeding, China Agricultural University, Beijing 100193, China

*Author for correspondence: yingfu@cau.edu.cn
†Senior author

Z.Q and Y.F. conceived the project. Z.Q., H.S., F.G., W.L., C.L., S.W., B.Z., L.Z., and S.Z. performed the experiments. Z.Q. wrote the manuscript. Y.F., X.W., J.L., F.Q., and Y.Z. revised the manuscript and all authors discussed and approved the manuscript.
The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/General-Instructions) is: Ying Fu (yingfu@cau.edu.cn).

Letter

Dear Editor,

Lignin is a phenylpropanoid-derived polymer that is directly deposited on the secondary walls of specialized cells, such as vessel elements and fibers, in plants. Lignification has vital roles in mechanical support, long-distance water transport, and plant defense (Barros et al., 2015). However, lignin is undesirable for biotechnological applications because its covalent interaction with cell wall polysaccharides limits the enzymatic digestion of agricultural biomass feedstocks (Torney et al., 2007). A hierarchical transcriptional network comprising various transcription factors (TFs), including NACs (NAM, ATAF, and CUC) and MYBs (myeloblastosis-related proteins), controls lignin biosynthesis in Arabidopsis (*Arabidopsis thaliana*). In this network, different MYBs act as activators (e.g. MYB58 and MYB63) or repressors (e.g. MYB4 and MYB32) of lignin biosynthesis genes (LBGs) and these MYBs are also downstream targets of MYB46 and MYB83 (Xie et al., 2018). In maize (*Zea mays* L.), ZmMYB31 and ZmMYB42 were repressors of LBGs (Sonbol et al., 2009; Fornale et al., 2010). However, the upstream regulation mechanism is still unrevealed. Here, we report that ZmMYB69 is a regulatory factor at the upper level of ZmMYB31 and ZmMYB42 in the hierarchical network that controls lignin biosynthesis in maize. We provide evidence that ZmMYB69 is a transcriptional activator and directly targets *ZmMYB31* and *ZmMYB42* promoters. Thereafter, it can repress lignin biosynthesis by activating *ZmMYB31* and *ZmMYB42* expression.

In this study, we overexpressed UBI-driven *ZmMYB69* in maize ND101 inbred plants. Two lines (*OE2* and *OE3*) were obtained, which displayed reduced plant height (Supplemental Figure S1) and decreased vascular bundle cell wall thickness (Figure 1, A and B). By measuring the lignin content in the cell wall (Foster et al., 2010), we detected significantly reduced lignification in the overexpression lines compared with that in ND101 (Figure 1C). In contrast, in *ZmMYB69* loss-of-function lines generated by the CRISPR/Cas9 technique (*Cas9-16* and *Cas9-18*), we observed thicker cell walls and higher lignin content, but no visible growth defect was detected (Figure 1, A–C and Supplemental Figure

Received February 11, 2022. Accepted April 28, 2022. Advance access publication May 28, 2022

附录

https://doi.org/10.1093/plphys/kiac237 PLANT PHYSIOLOGY 2022: 189: 2227–2243

Plant Physiology®

Research Article

Receptor-like protein kinase BAK1 promotes K^+ uptake by regulating H^+-ATPase AHA2 under low potassium stress

Zhi-Fang Wang ,[1] Zhong-Mei Xie,[1] Ya-Lan Tan,[1] Jia-Ying Li,[1] Feng-Liu Wang ,[1] Dan Pei ,[1] Zhen Li [1] Yan Guo ,[1] Zhizhong Gong ,[1,2] and Yi Wang [1,*,†]

1 State Key Laboratory of Plant Physiology and Biochemistry (SKLPPB), College of Biological Sciences, China Agricultural University, Beijing 100193, China

2 School of Life Sciences, Institute of Life Science and Green Development, Hebei University, Baoding, Hebei 071002, China

*Author for correspondence: yiwang@cau.edu.cn

†Senior author

Y.W. designed the research. Z.F.W., Z.M.X., Y.L.T., J.Y.L., and F.L.W. conducted the experiments. D.P., Z.L., Z.G., and Y.G. provide experimental support. Z.F.W. and Y.W. wrote and revised the article.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/general-instructions) is Yi Wang (yiwang@cau.edu.cn).

Abstract

Potassium (K^+) is one of the essential macronutrients for plant growth and development. However, the available K^+ concentration in soil is relatively low. Plant roots can perceive low K^+ (LK) stress, then enhance high-affinity K^+ uptake by activating H^+-ATPases in root cells, but the mechanisms are still unclear. Here, we identified the receptor-like protein kinase Brassinosteroid Insensitive 1-Associated Receptor Kinase 1 (BAK1) that is involved in LK response by regulating the Arabidopsis (*Arabidopsis thaliana*) plasma membrane H^+-ATPase isoform 2 (AHA2). The *bak1* mutant showed leaf chlorosis phenotype and reduced K^+ content under LK conditions, which was due to the decline of K^+ uptake capacity. BAK1 could directly interact with the AHA2 C terminus and phosphorylate T858 and T881, by which the H^+ pump activity of AHA2 was enhanced. The *bak1 aha2* double mutant also displayed a leaf chlorosis phenotype that was similar to their single mutants. The constitutively activated form AHA2Δ98 and phosphorylation-mimic form $AHA2^{T858D}$ or $AHA2^{T881D}$ could complement the LK sensitive phenotypes of both *aha2* and *bak1* mutants. Together, our data demonstrate that BAK1 phosphorylates AHA2 and enhances its activity, which subsequently promotes K^+ uptake under LK conditions.

Introduction

As one of macronutrients, potassium (K^+) is essential for plant growth and development. Plants need to absorb a large amount of K^+ from external environment to maintain normal life activities. Potassium constitutes 2%–10% of plant dry weight. The cytoplasmic K^+ concentration in living plant cells can reach 100–200 mM (Clarkson and Hanson, 1980; Sodek et al., 1980; Leigh and Wyn Jones, 1984; Maathuis, 2009). However, in soils the available K^+ for plants is relatively low and the concentration is typically within micromolar range (Schroeder et al., 1994; Maathuis, 2009). Therefore, plants often suffer low K^+ (LK) stress in natural environment. It is known that plants can sense and transduce the LK stress signal, and actively respond to LK stress for their survival via physiological and morphological alteration (Xu et al., 2006; Wang and Wu, 2013; Ragel et al., 2015; Wang and Wu, 2015, 2017).

Received April 08, 2022. Accepted May 01, 2022. Advance access publication May 23, 2022