

申 报	系列：教学科研 并重型
	专业：植物学
	职称：教授

业绩成果材料

（申报人的业绩成果材料包括论文、科研项目、获奖以及其他成果等）

单 位（二级单位） 生命科学学院

姓 名 梁祥修

材料核对人：

单位盖章：

核对时间：

华南农业大学制

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2023年拟推荐省级教学改革项目和校级教学改革拟立项项目名单

序号	项目名称	项目负责人	拟立项级别	备注
1	高阶思维视域下《种子生物学》“四维融合”混合式教学模式改革与实践	周玉亮	校重点项目	拟推荐省级
2	新林科视域下森林培育学知识图谱课程建设与教学模式创新	邱权	校重点项目	拟推荐省级
3	一流专业建设背景下风景园林规划设计课程教学改革研究	陈崇贤	校重点项目	拟推荐省级
4	一流农科高校基础实验课程思政教学一体化改革与实践——以大学物理实验课程为例	劳媚媚	校重点项目	拟推荐省级
5	双一流高校“科-教-思”融合培养学生高阶思维的实验教学改革研究——以遗传学实验为例	李楠	校重点项目	拟推荐省级
6	工程结构设计软件课程的“融合+分层”教学	李文雄	校重点项目	拟推荐省级
7	基于竞赛和创新方法提升大学生创新能力的实证研究	易欣	校重点项目	拟推荐省级
8	基于创新创业能力培养的“赛教融合”《养羊学》课程改革与实践	柳广斌	校重点项目	拟推荐省级
9	人工智能赋能生态化大学英语混合教学改革研究	苏君	校重点项目	拟推荐省级
10	基于创新能力培养的《电路实验》教学改革研究	王建华	校重点项目	拟推荐省级
11	新时代高校思政课“问题链”教学模式研究——聚焦《习近平新时代中国特色社会主义思想概论》课程	何艳玲	校重点项目	拟推荐省级
12	三产融合理论在《茶叶生物化学》中的应用	张钰乾	校重点项目	拟推荐省级
13	工程认证背景下基于知识图谱的新工科一流专业建设和提升的研究与实践	王金凤	校重点项目	拟推荐省级
14	融合数据分析思维和学科交叉的《线性代数》课程教学创新与实践	张伟峰	校重点项目	拟推荐省级
15	基于创新能力培养的统计学专业数据分析类实验课程改革探索与实践	周燕	校重点项目	拟推荐省级
16	基于知识图谱的农业院校课程思政建设探索——以公共数学基础课为例	张娜	校招标项目	拟推荐省级
17	基于新兽医人才培养的《分子生物学》课程改革与实践探索	沈永义	校重点项目	拟推荐省级
18	思政视角下《国际金融》课程教学改革与实践	周超	校重点项目	拟推荐省级
19	新农科背景下基于“数字标本”的智慧植保实验体系研究	李云锋	校重点项目	拟推荐省级
20	低碳农业背景下基于一特两驱教学模式的环境土壤学课程体系构建	林庆祺	校重点项目	拟推荐省级
21	“双一流”建设视野下安全教育模式嵌入环境化学实验室课程体系的实践与优化	高婷	校重点项目	拟推荐省级
22	“三台协同，以美育人”——以课程教学为基础的高校舞蹈美育建设研究	郑琳喆	校重点项目	拟推荐省级
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53	课程思政与“五育并举”融合发展的高校足球课程改革与实践研究	陈存志	校一般项目	
54	思政引导的体育课程内容体系改革与实践——以瑜伽课为例	何灵捷	校一般项目	
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65	《园艺种质资源与分类》实验教学内容体系优化的研究与实践	张志珂	校一般项目	
66	“真人+数字人”的智能教学模式探索与实践——以《数据结构》课程为例	梁云	校一般项目	
67	数字化背景下《大学生心理健康教育》课程思政建设与实践	严颖	校一般项目	
68	基于创新型人才培养目标对《海洋环境化学》的教学改革研究	公晗	校一般项目	
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華南農業大學

本科教学质量工程与教育教学改革项目

开题论证报告书

项 目 名 称 : 《植物学实验》“课程思政”的探索与实践

项 目 类 型 : 一般项目

项 目 级 别 : 校级

项 目 负 责 人 : 梁祥修

联 系 电 话 : 18910972541

所 在 单 位 : 生命科学学院

填 写 时 间 : 2024 年 3 月 14 日

华南农业大学本科生院制

二〇二四年三月

五、项目经费使用计划

(一) 按《华南农业大学本科教学质量与教学改革工程项目建设管理办法》第四章第十九条和附件5(2023年度立项质量工程项目与教改项目学校资助标准)填写。

(二) 在线开放课程项目不用填写。

(三) 企业1:1配套的项目须按照配套后的经费综合做预算。

年度	经费(万元)	支出用途说明
2024年	0.08	用于支出材料打印费
2025年	0.1	用于支出文献资料查阅费用
2026年	0.22	用于支出实验课过程中的耗材支出
合 计	0.4	

六、项目负责人承诺

我承诺遵守广东省和学校本科高校教学质量与教学改革工程项目管理有关规定,认真开展研究工作、经费专款专用。提交年度计划和进展报告,取得预期成果,实现预期目标,按期结题验收。

负责人签字: 梁祥明
2024年3月20日

七、项目所在单位审核意见

同意立项

单位领导签名(盖章): 李国辉
2024年3月20日



广东省教育厅

粤教高函〔2024〕9号

广东省教育厅关于公布 2023 年度广东省 本科高校教学质量与教学改革工程建设 项目立项名单的通知

各本科高校：

按照《广东省教育厅关于开展 2023 年度广东省本科高校教学质量与教学改革工程项目申报推荐工作的通知》等文件安排，经学校遴选推荐、省教育厅审核、公示等环节，现将 2023 年省本科高校质量工程建设项目立项名单予以公布，并就有关事项通知如下：

一、立项情况

确定立项建设省级实验教学示范中心 28 个、校企联合实验室 29 个、科产教融合实践教学基地 71 个、大学生社会实践教学基地 35 个、教师教学发展中心 5 个、课程教研室 167 个、现代产业学院 32 个、专项人才培养计划 62 项、高等教育教学改革项目 802 项。具体立项名单见附件。

二、项目管理

（一）本次公布项目均为省质量工程建设项目，建设项目经学校组织建设、校内结题并通过省教育厅统一组织项目验收后，正式认定为省级项目。

（二）项目正式实施前，请确保已对项目建设目标、建设举措、预期成果、建设进度安排等进行科学论证，论证专家应不少于5人，且至少有三分之一来自外校。论证后的目标、任务等将作为项目结题验收时的重要依据。

（三）项目日常管理由学校主管部门负责，学校应统筹做好项目中期检查、校内结题验收等工作。校内结题时，邀请校外评审专家人数不得少于专家总人数的三分之二。满足以下条件的项目，经学校正式申请，可以参与省教育厅统一组织的项目验收：

- 1.项目已完成立项时设定的主要建设任务和目标；
- 2.项目已取得标志性建设成果，且该成果已在教学实践中得到检验和有效应用；
- 3.已按照要求完成项目校内结题；
- 4.符合当年度省统一验收规定的其他条件。

各校质量工程建设项目管理情况，将作为学校下一年度项目立项限额的参考依据。

（四）项目实施过程中，其名称、建设内容（任务）、建设目标、建设周期、主要负责人、预期成果等发生重大变更的，需由时任项目负责人在发生变更后及时提出，经学校项目主管部门审核后由学校正式来函说明原因；擅自变更上述内容的，验收评定

时列为不通过。

三、其他事项

（一）2023 年度各校向省教育厅推荐并获得立项的项目，学校须将项目校内评审、推荐及论证相关材料妥善保存，留底备查。

（二）各校要统筹本校“冲补强”提升计划资金及自有资金对立项项目予以资助，项目获得学校资助情况将作为项目结题验收时重要考察因素之一。如项目建设中取得具有推广价值的优秀成果，请及时形成书面材料报省教育厅高教处。

联系人：李成军、窦月月，联系电话：020-37626882。

附件：2023 年度广东省本科高校教学质量与教学改革工程建设项目立项名单



509	高等教育教学改革项目	暨南大学	“一体五驱”工程认证专业课程“多维融合”教学创新体系的探索与实践—以“包装振动与冲击”课程为例	杨松平
510	高等教育教学改革项目	暨南大学	融入国产操作系统和OBE理念的操作系统原理课程教学改革与实践	张继连
511	高等教育教学改革项目	暨南大学	“思政教育”融入大学生专业实习教学的体系构建与路径探索	赵建刚
512	高等教育教学改革项目	华南农业大学	一流农科高校基础实验课程思政教学一体化改革与实践 —以大学物理实验课程为例	劳媚媚
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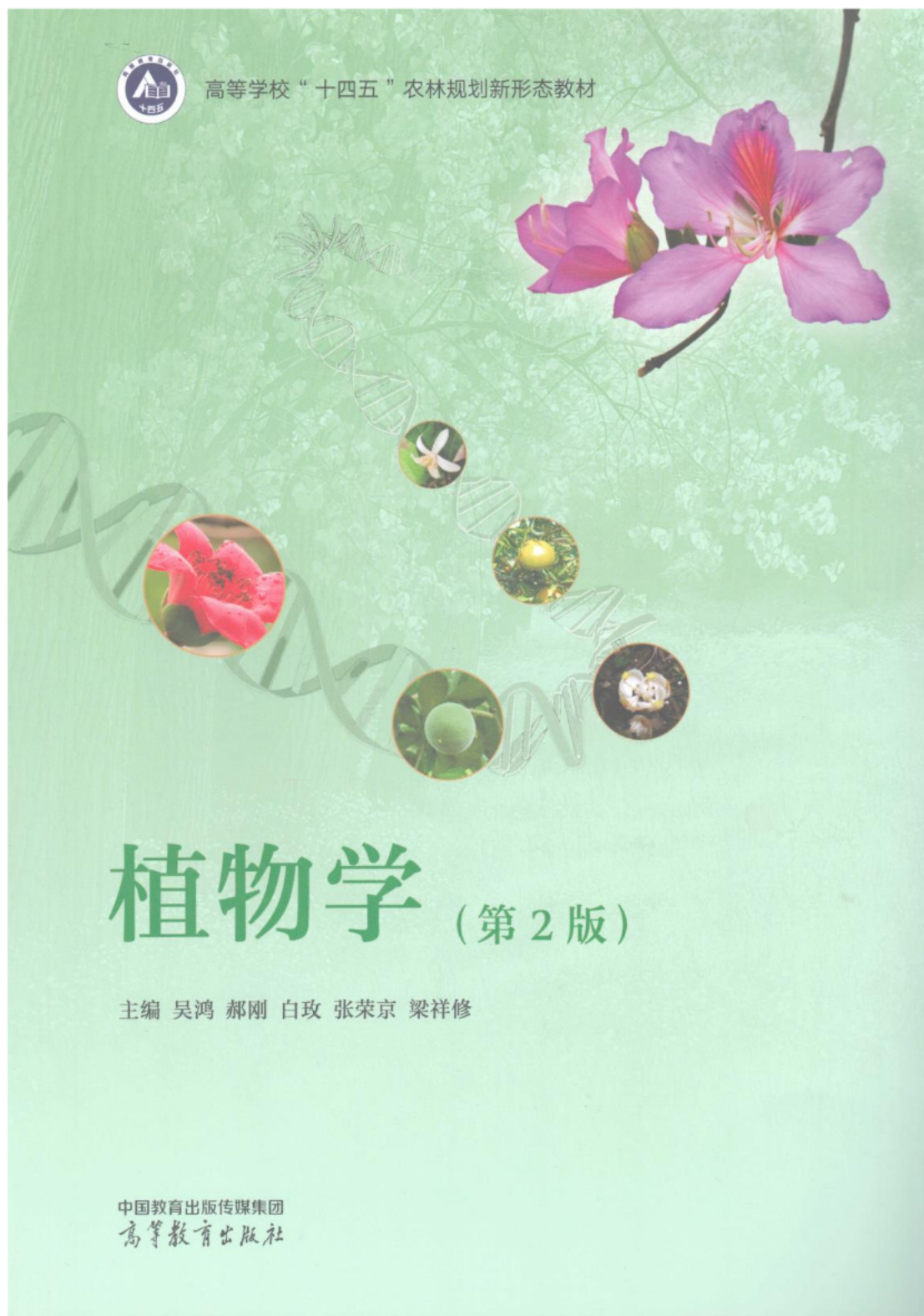
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本课程依照高等农林院校本科教学改革的方向和人才培养目标编写,注重吸收植物近十年来学科发展的新成果,适应“新农科”建设,推广产、学、研结合。教材力求广泛“面”农业产业,兼重“新”学科,主要以粮食、粮食、木材、能源、花卉等经济植物及地域特色植物为代表,介绍植物形态与结构特征和个体发育过程,植物的基本类型和主要类群的植物多样性。全除按植物学外,还分其分为14,内容包括种子植物、蕨类植物、藻菌植物、被子植物的营养器官、被子植物的繁殖和繁殖器官、被子植物的营养器官和生殖器官、植物界的类群与分类、被子植物分类的形态学基础知识、被子植物及其主要类群。

本书可作为高等农林院校植物生产类、生物科学类及相关专业本科生的教材,也可作为研究生、教师、农林科技工作者的参考用书。

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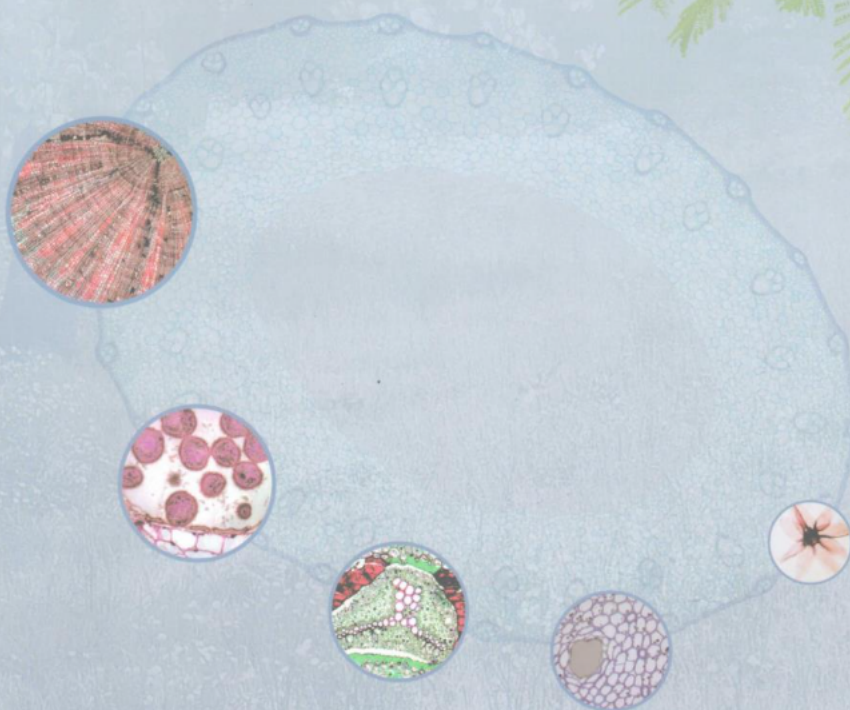


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植物学实验指导

(第2版)

主编 吴鸿 郝刚 白玫 张荣京 梁祥修



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内容提要

本书的编写依据高等农业院校本科教学的培养目标,结合新时期植物学实验学时调整安排而设计编排。

书中内容注重理论联系实际,强调培养学生独立观察、操作的能力。书中的实验材料多选取华南地区的活体材料,力求紧密联系农林生产实践。全书分为认知性实验、综合性实验和附录三个部分。认知性实验部分选编了12个基础性实验,内容包括被子植物的形态结构特征、植物界的基本类群介绍以及被子植物分类概述。综合性实验部分设计了7个拓展、探究性项目,均是围绕植物的结构与功能的适应关系这个主题。附录部分介绍植物学实验、实习常用的基础知识和工具,如标本的采集制作、植物制片法、常用试剂的配制等。

本书适合于高等农业院校农学、林学、生物等相关专业使用,亦可作为研究生、教师、科技工作者的参考用书。

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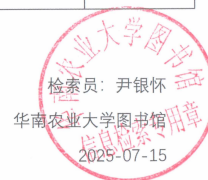
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2	The secret of fertilization in flowering plants unveiled	Science Bulletin 出版年: 2018 卷期: 63 页码: 408-410 文献号: 文献类型: Editorial Material	第一作者	B 类	Chinese Academy of Sciences	SCI	IF2-year=6.277 IF5-year=5.32 (2018)	综合性期刊 3 区 Top 期刊: 否 (2018)
3	Ligand-triggered de-repression of Arabidopsis heterotrimeric G proteins coupled to immune receptor kinases	Cell Research 出版年: 2018 卷期: 28 5 页码: 529-543 文献号: 文献类型: Article	1	T2 类	Chinese Academy of Sciences	SCI	IF2-year=17.848 IF5-year=18.448 (2018)	生物 1 区 Top 期刊: 是 (2018)

4	Receptor-like cytoplasmic kinases: Central players in plant receptor kinase-mediated signaling	Annual Review of Plant Biology 出版年: 2018 卷期: 69 页码: 267-299 文献号: 文献类型: Review	第一作者	T2 类	Chinese Academy of Sciences	SCI	IF2-year=18.918 IF5-year=25.776 (2018)	生物 1 区 Top 期刊: 是 (2018)
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6	A Phytophthora capsici RXLR effector targets and inhibits the central immune kinases to suppress plant immunity	New Phytologist 出版年: 2021 卷期: 232 1 页码: 264- 278 文献号: 文献类型: Article	1	T2 类	China Agricultural University	SCI	IF2-year=10.323 IF5-year=10.768 (2021)	生物学 1 区 Top 期刊: 是 (2021)

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2	Rice extra-large G proteins play pivotal roles in controlling disease resistance and yield-related traits	New Phytologist 出版年: 2022 卷期: 234 2 页码: 607-617 文献号: 文献类型: Article	共同通讯作者	T2 类	China Agricultural University	SCI	IF2-year=9.4 IF5-year=10.5 (2022)	生物学 1 区 Top 期刊: 是 (2022)
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4	Extra-large G proteins regulate disease resistance by directly coupling to immune receptors in <i>Nicotiana benthamiana</i>	Phytopathology Research 出版年: 2022 卷期: 4 1 页码: - 文献号: 49 文献类型:	通讯作者	A 类	South China Agricultural University	SCI	IF2-year=3.4 IF5-year=4.2 (2022)	农林科学 2 区 Top 期刊: 否 (2022)
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7	A Pair of Soybean Maltectin-like Domain-containing Receptor-like Kinases Jointly Regulate Pattern-triggered Immunity by Forming Hetero-oligomers	Phytopathology Research 出版年: 2024 卷期: 6 1 页码: - 文献号: 13	共同通讯作者 (倒数第一)	A 类	South China Agricultural University	SCI	IF2-year=3.5 IF5-year=3.9 (2024)	农林科学 2 区 Top 期刊: 否 (2025)

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9	Metformin blocks BIK1-mediated CPK28 phosphorylation and enhances plant immunity	Journal of Advanced Research 出版年: 2024 卷期: 68 页码: 31-41 文献号: 文献类型: Article	共同通讯作者	T2 类	South China Agricultural University	SCI IF2-year=13.0 IF5-year=11.6 (2024)	综合性期刊 1 区 Top 期刊: 是 (2025)
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Arabidopsis heterotrimeric G proteins regulate immunity by directly coupling to the FLS2 receptor

Xiangxiu Liang^{1†}, Pingtao Ding^{2†}, Kehui Lian², Jinlong Wang¹, Miaomiao Ma¹, Lin Li³, Lei Li¹, Meng Li¹, Xiaojuan Zhang¹, She Chen³, Yuelin Zhang^{2*}, Jian-Min Zhou^{1*}

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Abstract The Arabidopsis immune receptor FLS2 perceives bacterial flagellin epitope flg22 to activate defenses through the central cytoplasmic kinase BIK1. The heterotrimeric G proteins composed of the non-canonical G α protein XLG2, the G β protein AGB1, and the G γ proteins AGG1 and AGG2 are required for FLS2-mediated immune responses through an unknown mechanism. Here we show that in the pre-activation state, XLG2 directly interacts with FLS2 and BIK1, and it functions together with AGB1 and AGG1/2 to attenuate proteasome-mediated degradation of BIK1, allowing optimum immune activation. Following the activation by flg22, XLG2 dissociates from AGB1 and is phosphorylated by BIK1 in the N terminus. The phosphorylated XLG2 enhances the production of reactive oxygen species (ROS) likely by modulating the NADPH oxidase RbohD. The study demonstrates that the G proteins are directly coupled to the FLS2 receptor complex and regulate immune signaling through both pre-activation and post-activation mechanisms.

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Introduction

As an intensely studied Pattern Recognition Receptor (PRR) in plants, FLS2 serves as an excellent model understanding plant innate immune signaling and receptor kinases in general (**Macho and Zipfel, 2014**). It forms a dynamic complex with the co-receptor BAK1 and the receptor-like cytoplasmic kinase BIK1 to perceive a conserved bacterial flagellar epitope, flg22, to activate a variety of defense responses (**Chinchilla et al., 2007; Heese et al., 2007; Lu et al., 2010; Zhang et al., 2010; Sun et al., 2013**). Stability of FLS2 and BIK1 is subject to regulation by ubiquitin-proteasome system and a calcium-dependent protein kinase (**Lu et al., 2011; Monaghan et al., 2014**). We and others previously showed that BIK1 directly phosphorylates the NADPH oxidase RbohD to prime flg22-induced reactive oxygen species (ROS; **Kadota et al., 2014; Li et al., 2014**).

Heterotrimeric G proteins are central for signaling in animals (**McCudden et al., 2005; Oldham et al., 2008**), which contain hundreds of G Protein-Coupled Receptors (GPCRs). In the pre-activation state, the GDP-bound G α interacts with the G $\beta\gamma$ dimer to form a heterotrimer. Upon activation by GPCR, G α exchanges GDP for GTP, resulting in the activation of the heterotrimer. The activated G α and G $\beta\gamma$ dissociate from each other to regulate downstream effectors. Plants contain canonical G α (encoded by *GPA1* in Arabidopsis), G β (encoded by *AGB1* in Arabidopsis), G γ proteins (encoded by *AGG1*, *AGG2*), and a non-canonical G γ (encoded by *AGG3* in Arabidopsis) (Urano and Jones, 2013). Plants additionally encode extra-large G proteins (XLGs, encoded by *XLG1*, *XLG2*, and *XLG3* in Arabidopsis) that carry a variable N-terminal domain and a C-terminal G α domain (**Lee and**



Research Highlight

The secret of fertilization in flowering plants unveiled

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As recapitulated in the famous Chinese fairy tale *Journey to the West*, the Buddhist monk Xuanzang of the Tang Dynasty (Tang-seng) took a heroic journey in a quest for India Buddhist sacred scriptures. The long and dangerous journey was made possible only with the help of the powerful Monkey King, who had been pinned down under a mountain by the Buddha as a punishment for his prior misdemeanor. The Buddha had to secure the mountain with a magic paper seal so that the Monkey King would not break loose. The Monkey King burst out from the mountain as soon as Tangseng lifted the seal, so that he could escort Tangseng through the journey (Fig. 1).

To some extent, the secret process of fertilization in flowering plants has much in common with this legendary story. Unlike animals, the sperm cells of angiosperm are unable to swim and must be transported to female gametes to accomplish the sexual reproduction. These sperm cells are enclosed as a cargo in a pollen grain [1]. Upon landing on the stigma, the tip of female reproductive organ, the pollen grain germinates and forms a growing pollen tube that travels a long distance through the female tissue to reach ovule, where it ruptures to release sperms and fertilizes the egg cell inside ovule (Fig. 2). The process takes place with remarkable precision and includes guided growth of pollen tube, prevention of pre-mature rupture of pollen tube before reaching the ovule, accurate localization of ovule opening, repression of pollen tube growth upon arrival to the ovule, and the rupture of pollen tube at the final stage [2]. Sophisticated communications between male and female reproductive tissues are crucial for the execution of each step, and any miscommunication results in failure of fertilization and aborted seed-set. A number of small peptides produced by pollen tube and female tissues serve as signals coordinating this complex process. For instance, small CYSTEINE-RICH PEPTIDES (CRPs), such as tomato LAT52 and STIG are known to regulate pollen tube growth [3,4]. The *Arabidopsis* LUREs [5] and maize ES1–4 [6] which are also CRPs, guide pollen tube growth toward the ovule. Members of another class of CRPs called RAPID-ALKALIZATION FACTORS (RALFs) have been reported to arrest pollen tube growth once inside the ovule [7–9]. Identification of peptides and their receptors controlling pollen tube journey is a major task in the field of plant reproduction research.

Synergid cells, a pair of cells neighboring the egg cell, are known to be a key source of female signals. LUREs [5] and ES1–4 [6]

produced by synergid cells are key attractants for pollen tube guidance in *Arabidopsis* and maize respectively. Several Leucine-Rich Receptor-Like Kinases (LRR-RLKs) including PRKs and MDIS1, and MIK1/2 likely form a receptor complex for the perception of LUREs [10]. Two closely related receptor-like cytoplasmic kinase (RLCK) named LOST IN POLLEN TUBE GUIDANCE 1 (LIP1) and LIP2 are required for LURE-regulated pollen tube guidance [11], likely by acting downstream of the LURE receptor complex.

The *Arabidopsis* RLK protein FERONIA (FER), which belongs to the *Catharanthus roseus* RLK-like (CrRLK1L) family, also plays key role in pollen tube reception [12]. FER is highly expressed in synergid cell plasma membrane and is required for the repression of pollen tube elongation in the ovule [7]. Later research discovered FER as a major receptor for RALFs to suppress cell elongation [8]. Whether specific members of RALFs regulate the FER-mediated pollen tube growth-arrest remains unknown.

Controlled rupture of pollen tube tip is not only required for the release of sperm cells in the ovule, but also ensure pollen tube reaching the ovule without premature rupture. ANXUR1 (ANX1) and ANX2, two closely-related CrRLK1L family members localized at the tip of pollen tube, are required for the integrity of pollen tube [13,14]. The pollen tube of *anx1 anx2* double mutant bursts spontaneously after pollen germination and is male sterile. These findings suggest an involvement of transmembrane signaling in the control of pollen tube rupture. Consistent with this notion, the RLCK protein MARIS (MRI) and a pair of NADPH oxidases have been shown to act downstream for the ANXs-mediated suppression of pollen tube rupture [15,16]. It is not known, however, whether ANX1/2 are receptors or part of the receptor complex perceiving an unknown ligand to prevent premature rupture. Moreover, it is unknown how the ANX-mediated suppression is removed to allow pollen tube rupture in the ovule.

A newly published study sheds light on these important questions. Qu and colleagues show that, a pair of CrRLK1L members are essential to prevent premature rupture of pollen tube [17]. Inspired by the Monkey King story, the authors name these proteins Buddha's Paper Seal 1 (BUPS1) and BUPS2. Several lines of evidence indicate that BUPS1/2 and ANX1/2 act together to control pollen tube integrity. The *bups1/2* double mutants are completely sterile, and their pollen grains phenocopy that of *anx1/2* double mutants and burst spontaneously after germination. Like ANX1/2, BUPS1/2 are expressed in pollen grains and pollen tubes.

Because BUPS1/2 and ANX1/2 belong to the CrRLK1L family and are homologous to FER, the authors hypothesized that BUPS1/2

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ARTICLE OPEN

Ligand-triggered de-repression of *Arabidopsis* heterotrimeric G proteins coupled to immune receptor kinasesXiangxiu Liang^{1,2}, Miaomiao Ma^{1,3}, Zhaoyang Zhou¹, Jinlong Wang¹, Xinru Yang⁴, Shaofei Rao¹, Guozhi Bi¹, Lin Li⁵, Xiaojuan Zhang¹, Jijie Chai⁴, She Chen⁵ and Jian-Min Zhou^{1,3}

Arabidopsis heterotrimeric G proteins regulate diverse processes by coupling to single-transmembrane receptors. One such receptor is the FLS2 receptor kinase, which perceives bacterial flagellin epitope flg22 to activate immunity through a class of cytoplasmic kinases called BIK1/PBLs. Unlike animal and fungal heterotrimeric G proteins that are activated by a ligand-induced guanine nucleotide exchange activity of seven-transmembrane G protein-coupled receptors (GPCRs), plant heterotrimeric G proteins are self-activating. How plant receptors regulate heterotrimeric G proteins in response to external ligands remains unknown. Here we show that RGS1, a GTPase accelerating protein, maintains *Arabidopsis* G proteins in an inactive state in complex with FLS2. Activation of FLS2 by flg22 induces a BIK1/PBL-mediated phosphorylation of RGS1 at Ser428 and Ser431 and that promotes RGS1 dissociation from the FLS2-G protein complex. This relieves G proteins from the RGS1-mediated repression and enables positive regulation of immune signaling. We additionally show that RGS1 is similarly regulated by multiple immune receptors. Our results uncover ligand-induced de-repression as a mechanism for G protein signaling in plants that is distinct from previously reported mechanism underlying the activation of heterotrimeric G proteins in other systems.

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INTRODUCTION

Heterotrimeric G proteins are universal signaling modules in eukaryotic organisms, including animals, plants and fungi. They regulate transmembrane signaling by coupling to cell surface-localized receptors. The animal and fungal heterotrimeric G proteins are directly regulated by seven-transmembrane G protein-coupled receptors (GPCRs). In the resting state, a GDP-bound G α associates with a G $\beta\gamma$ dimer to form an inactive trimer. Upon stimulation by extracellular ligands, GPCRs act as guanine nucleotide exchange factors (GEFs) to promote GDP-GTP exchange in G α to activate the G proteins. The GTP-bound G α dissociates from the G $\beta\gamma$ dimer, and each entity goes on to regulate different downstream target referred to as “effectors”. Hydrolysis of GTP by the intrinsic GTPase activity of G α allows cycling of G α back to the GDP-bound resting state.^{1,2} The GTP hydrolysis is enhanced by the regulator of G protein signaling protein (RGS), a GTPase accelerating protein (GAP).^{2,3}

The *Arabidopsis* genome encodes four G α proteins (GPA1, XLG1, XLG2, and XLG3), one G β protein (AGB1), and three G γ proteins (AGG1, AGG2, and AGG3).⁴ Among these, GPA1 is a canonical G α , whereas XLG1, XLG2, and XLG3 are non-canonical G α proteins that contain an N-terminal domain of unknown function in addition to the C-terminal G α domain. Plant G α proteins also undergo GDP- and GTP-bound cycle, and the GTPase activity of plant G α proteins is similarly enhanced by RGS proteins. *Arabidopsis* contains a single RGS1 protein that negatively regulates GPA1-mediated signaling through its GAP activity.^{5,6} Plant heterotrimeric G

proteins have been shown to associate with receptor kinases (RKs), receptor-like kinases (RLKs), or receptor-like proteins (RLPs), which are all single-transmembrane proteins. The maize RLP FEA2 associates with the G α protein CT2 to maintain shoot apical meristem.⁷ The soybean RK NFR1 interacts with G α proteins to control nodulation.⁸ The *Arabidopsis* RK ERECTA genetically interacts with heterotrimeric G protein components to regulate disease resistance.^{9,10} We have shown recently that plant heterotrimeric G proteins are associated with and regulated by immune receptor kinase FLS2.¹¹ However, these plant receptors are not known to act as GEFs. Moreover, plant G α proteins are self-activating and can bind GTP in the absence of GEFs.^{12,13} How plant receptor kinases regulate heterotrimeric G proteins remains poorly understood.

Immune RKs FLS2, EFR, LYK5, and PEPRs are pattern recognition receptors (PRRs) that recognize microbe- or plant-derived molecular patterns including the bacterial flagellin epitope flg22, elongation factor Tu epitope elf18, fungal cell wall component chitin, and plant elicitor peptides (Peps), triggering a series of immune responses culminated in disease resistance against diverse pathogens.^{14–17} Among these, FLS2 has been extensively studied and serves as a model to understand RK-mediated signaling, particularly the regulation of heterotrimeric G proteins. Upon flg22 binding, FLS2 rapidly recruits its co-receptor BAK1, a receptor-like kinase, to form an active receptor complex and initiates immune signaling.^{18,19} Downstream of FLS2, receptor-like cytoplasmic kinase family VII (RLCKVII) members BIK1 and PBS1-

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Receptor-Like Cytoplasmic Kinases: Central Players in Plant Receptor Kinase–Mediated Signaling

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Keywords

receptor-like cytoplasmic kinases, ROS, reactive oxygen species, MAP kinases, mitogen-activated protein kinases, plant immunity, growth, development, abiotic stresses

Abstract




Receptor kinases (RKs) are of paramount importance in transmembrane signaling that governs plant reproduction, growth, development, and adaptation to diverse environmental conditions. Receptor-like cytoplasmic kinases (RLCKs), which lack extracellular ligand-binding domains, have emerged as a major class of signaling proteins that regulate plant cellular activities in response to biotic/abiotic stresses and endogenous extracellular signaling molecules. By associating with immune RKs, RLCKs regulate multiple downstream signaling nodes to orchestrate a complex array of defense responses against microbial pathogens. RLCKs also associate with RKs that perceive brassinosteroids and signaling peptides to coordinate growth, pollen tube guidance, embryonic and stomatal patterning, floral organ abscission, and abiotic stress responses. The activity and stability of RLCKs are dynamically regulated not only by RKs but also by other RLCK-associated proteins. Analyses of RLCK-associated components and substrates have suggested phosphorylation relays as a major mechanism underlying RK-mediated signaling.

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A malectin-like receptor kinase regulates cell death and pattern-triggered immunity in soybean

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Abstract

Plant cells can sense conserved molecular patterns through pattern recognition receptors (PRRs) and initiate pattern-triggered immunity (PTI). Details of the PTI signaling network are starting to be uncovered in Arabidopsis, but are still poorly understood in other species, including soybean (*Glycine max*). In this study, we perform a forward genetic screen for autoimmunity-related *lesion mimic mutants (lmms)* in soybean and identify two allelic mutants, which carry mutations in *Glyma.13G054400*, encoding a malectin-like receptor kinase (RK). The mutants exhibit enhanced resistance to both bacterial and oomycete pathogens, as well as elevated ROS production upon treatment with the bacterial pattern flg22. Overexpression of *GmLMM1* gene in *Nicotiana benthamiana* severely suppresses flg22-triggered ROS production and oomycete pattern XEG1-induced cell death. We further show that *GmLMM1* interacts with the flg22 receptor FLS2 and its co-receptor BAK1 to negatively regulate flg22-induced complex formation between them. Our study identifies an important component in PTI regulation and reveals that *GmLMM1* acts as a molecular switch to control an appropriate immune activation, which may also be adapted to other PRR-mediated immune signaling in soybean.

Keywords cell death; *Glycine max*; lesion mimic mutant; malectin-like receptor kinase; pattern-triggered immunity

Subject Categories Immunology; Microbiology, Virology & Host Pathogen Interaction; Signal Transduction

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Introduction

Soybean is one of the major sources of oil and plant proteins worldwide. Its demand in food, feed, and industrial production has

increased stably along with the rapid expansion of the world's population. Soybean diseases, including bacterial blight, phytophthora root rot, and soybean rust, continuously cause great losses to soybean yield and quality worldwide. Traditional disease control mainly relies on chemical and breeding methods, which are sometimes outpaced by the evolution of pathogens. Thus, it is important to study the soybean immune system and to understand how soybean defends itself against pathogens (Whitham *et al*, 2016). Plants are equipped with two layers of immune perception systems: pattern-triggered immunity (PTI) and effector-triggered immunity (ETI; Jones & Dangl, 2006). Plant plasma membrane-localized pattern recognition receptors (PRRs) can sense the presence of pathogens through recognition of microbe-associated molecule, such as bacterial flg22 and *Phytophthora sojae* XEG1, to activate downstream PTI signaling (Chinchilla *et al*, 2006; Wang *et al*, 2018). Successful pathogens can evade plant resistance by secreting effector proteins to suppress plant PTI signaling. Plant intracellular nucleotide-binding and leucine-rich repeat receptors (NLRs) can recognize the presence of microbial effectors to trigger a much stronger ETI response, which is usually accompanied by hypersensitive response (HR; Dou & Zhou, 2012; Jones *et al*, 2016). Both layers of the plant immune system have been extensively studied in Arabidopsis and some crops, such as rice. However, the limited information on soybean immunity focuses mainly on ETI, few on PTI. For example, several NLRs have been cloned and characterized during the last decade (Whitham *et al*, 2016), including Rpg1b/Rpg1r that recognizes AvrB/AvrRpm1 from *Pseudomonas syringae* pv. *glycinea* (Psg) (Ashfield *et al*, 2014).

Reports of immune responses mediated by PRRs in soybean are scarce (Whitham *et al*, 2016). Although PTI is not as strong as ETI, it confers a much broader and moderate resistance to most microbes, with potentially lower growth and yield penalty. In plants, PRRs consist of receptor kinase (RK) and receptor protein (RP). RK contains a variable ectodomain potentially involved in ligand perception, a single transmembrane domain, and a cytoplasmic kinase domain for signal transduction. RP contains an

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A *Phytophthora capsici* RXLR effector targets and inhibits the central immune kinases to suppress plant immunity

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Key words: immune kinases, *Phytophthora capsici*, plant immunity, RLCK-VII, RXLR25.

Summary

- Receptor-like cytoplasmic kinase subfamily VII (RLCK-VII) proteins are the central immune kinases in plant pattern-recognition receptor (PRR) complexes, and they orchestrate a complex array of defense responses against bacterial and fungal pathogens. However, the role of RLCK-VII in plant–oomycete pathogen interactions has not been established. *Phytophthora capsici* is a notorious oomycete pathogen that infects many agriculturally important vegetables.
- Here, we report the identification of RXLR25, an RXLR effector that is required for the virulence of *P. capsici*. *In planta* expression of RXLR25 significantly enhanced plants' susceptibility to *Phytophthora* pathogens. Microbial pattern-induced immune activation in Arabidopsis was severely impaired by RXLR25. We further showed that RXLR25 interacts with RLCK-VII proteins.
- Using nine *rlck-vii* high-order mutants, we observed that RLCK-VII-6 and RLCK-VII-8 members are required for resistance to *P. capsici*. The RLCK-VII-6 members are specifically required for *Phytophthora* culture filtrate (CF)-induced immune responses. RXLR25 directly targets RLCK-VII proteins such as BIK1, PBL8, and PBL17 and inhibits pattern-induced phosphorylation of RLCK-VIIs to suppress downstream immune responses.
- This study identified a key virulence factor for *P. capsici*, and the results revealed the importance of RLCK-VII proteins in plant–oomycete interactions.

Introduction

Plants rely on their innate immune system to protect themselves from infection. Plant cells are equipped with two types of immune receptors, the cell-surface-localized pattern-recognition receptors (PRRs) and intracellular nucleotide-binding, leucine-rich repeat receptors (NLRs) that perceive microbial invasion and activate plant immunity. Pattern-recognition receptors can sense the invasion of pathogens through recognition of microbe-derived molecular patterns such as bacterial flg22, fungal chitin, and *Phytophthora sojae* XEG1 to activate the plant immune system (Chinchilla *et al.*, 2006; J. Wang *et al.*, 2018; Y. Wang *et al.*, 2018). Successful pathogens can overcome plant basal resistance by secreting a plethora of effector proteins to suppress plant immune signaling and facilitate host infection. Plant intracellular NLRs recognize the presence of microbial effectors and trigger a

second round of plant immunity to further amplify and strengthen the plant immune responses (Jones *et al.*, 2016; Zhou & Zhang, 2020). Rapid recognition of conserved molecular patterns by PRRs is the key step in the initiation of plant immune responses, and it confers broad resistance to most microbes. Arabidopsis receptor kinase (RK) FLS2 recognizes the bacterial flagellin epitope flg22 in the presence of the co-receptor BAK1 (Chinchilla *et al.*, 2006; Sun *et al.*, 2013). *Phytophthora sojae*-derived pattern XEG1 is recognized by *Nicotiana benthamiana* receptor protein (RP) RXEG1, which is in complex with the co-receptors NbBAK1 and NbSOBIR1 (J. Wang *et al.*, 2018; Y. Wang *et al.*, 2018). Pattern-recognition receptors form complexes with many key regulatory components such as receptor-like cytoplasmic kinases (RLCKs) (Lin *et al.*, 2013; Liang & Zhou, 2018), heterotrimeric G proteins (Liang *et al.*, 2016, 2018), and the NADPH oxidase RbohD (Kadota *et al.*, 2014; Li *et al.*, 2014), to activate a series of downstream immune responses, including production of reactive oxygen species

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Functional Diversification Analysis of Soybean Malectin/Malectin-Like Domain-Containing Receptor-Like Kinases in Immunity by Transient Expression Assays

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Plants have responded to microbial pathogens by evolving a two-tiered immune system, involving pathogen-associated molecular pattern (PAMP)-triggered immunity (PTI) and effector-triggered immunity (ETI). Malectin/malectin-like domain-containing receptor-like kinases (MRLKs) have been reported to participate in many biological functions in plant including immunity and resistance. However, little is known regarding the role of MRLKs in soybean immunity. This is a crucial question to address because soybean is an important source of oil and plant proteins, and its production is threatened by various pathogens. Here, we systematically identified 72 *Glycine max* MRLKs (GmMRLKs) and demonstrated that many of them are transcriptionally induced or suppressed in response to infection with microbial pathogens. Next, we successfully cloned 60 GmMRLKs and subsequently characterized their roles in plant immunity by transiently expressing them in *Nicotiana benthamiana*, a model plant widely used to study host-pathogen interactions. Specifically, we examined the effect of GmMRLKs on PTI responses and noticed that a number of GmMRLKs negatively regulated the reactive oxygen species burst induced by flg22 and chitin, and cell death triggered by XEG1 and INF1. We also analyzed the microbial effectors AvrB- and XopQ-induced hypersensitivity response and identified several GmMRLKs that suppressed ETI activation. We further showed that GmMRLKs regulate immunity probably by coupling to the immune receptor complexes. Furthermore, transient expression of several selected GmMRLKs in soybean hairy roots conferred reduced resistance to soybean pathogen *Phytophthora sojae*. In summary, we revealed the common and specific roles of GmMRLKs in soybean immunity and identified a number of GmMRLKs as candidate susceptible genes that may be useful for improving soybean resistance.

Keywords: soybean, malectin/malectin-like domain-containing receptor-like kinases, immune responses, PTI, ETI

Rice extra-large G proteins play pivotal roles in controlling disease resistance and yield-related traits

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Summary

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Key words: agronomic traits, disease resistance, plant immunity, rice, XLG protein.

- To better explore the potential of rice extra-large G (XLG) proteins in future breeding, we characterised the function of *OsXLG1*, *OsXLG2* and *OsXLG3* in disease resistance. Loss-of-function *Osxlg2* and *Osxlg3* mutants showed reduced resistance to the fungal pathogen *Magnaporthe oryzae*, whereas *Osxlg1* mutants were specifically compromised in resistance to the bacterial pathogen *Xanthomonas oryzae* pv *oryzae*.
- Consistent with their effects on rice blast resistance, mutations in *OsXLG2* and *OsXLG3* caused greater defects than did mutations in *OsXLG1* for chitin-induced defence responses. All three *OsXLGs* interacted with components of a surface immune receptor complex composed of *OsCERK1*, *OsRLCK176* and *OsRLCK185*.
- Further characterisation of yield-related traits showed that the *Osxlg3* mutants displayed reduced plant height, panicle length and 1000grain weight, whereas *Osxlg1* mutants exhibited increased plant height, panicle length and 1000-grain weight.
- Together the study shows the differential contributions of the three *OsXLG* proteins to disease resistance to fungal and bacterial pathogens, their yield-related traits and provides insights for future improvement of rice production.

Introduction

Rice is one of the most important food crop, and its demand is increasing along with the rapid expansion of the world's population. Improving the yield and quality are the major challenge of rice production. Rice yield is mainly controlled by a series of agronomic characteristics, including tiller number, grain number and grain size (Xing & Zhang, 2010). For the last decades, some genes and quantitative trait loci (QTLs) related to rice yield and quality have been identified and introduced into elite cultivars. With the changes in global climate and agricultural practices, rice diseases frequently occur. Rice production is severely threatened by a variety of pathogens, including fungal pathogen *Magnaporthe oryzae* (*M. oryzae*) and bacterial pathogen *Xanthomonas oryzae* pv *oryzae* (*Xoo*). *Magnaporthe oryzae* and *Xoo* respectively cause fungal blast and bacterial blast, which are devastating diseases for rice production. Plants rely on their innate immune system to detect and defend various invading pathogens. However, plant immunity often comes at a cost on plant growth and development. There is an urgent need to develop rice plants with broad-spectrum resistance and minimal yield penalty.

Heterotrimeric G protein complex composed of $G\alpha$, $G\beta$ and $G\gamma$ subunits is one of the major signal transducers in eukaryotic

cells. G proteins work as nodes for coordination of multiple biological processes (Pandey, 2019). In animals, the seven-transmembrane G protein coupled receptors (GPCRs) can perceive extracellular signals through their ectodomains and transmit the signal to the $G\alpha$ subunits, leading to $G\alpha$ s exchange GDP for GTP and resulting in the activation of G proteins. The activated $G\alpha$ s dissociate from $G\beta\gamma$ dimers and each function on their downstream effectors (Oldham & Hamm, 2008). Mammals (e.g. human) have 23 $G\alpha$ s, 5 $G\beta$ s and 12 $G\gamma$ s, which can form multiple heterotrimer combinations. By contrast, plants have fewer G protein isoforms. The Arabidopsis genome encodes one canonical $G\alpha$, three extra-large G (XLG) proteins, one $G\beta$ and three $G\gamma$ s (Stateczny *et al.*, 2016). There is one canonical $G\alpha$, three *XLG* genes, one $G\beta$ and three $G\gamma$ s in the rice genome (Urano & Jones, 2014; Stateczny *et al.*, 2016). *XLG* proteins are a subfamily of plant-specific $G\alpha$ proteins, which contain a C-terminal $G\alpha$ domain and an N-terminal extension (Lee & Assmann, 1999). *XLG* proteins exist in all higher plants with a larger number than the canonical $G\alpha$. Some lower plants, such as the moss *Physcomitrella patens*, lack the canonical $G\alpha$ and possess one *XLG* as the only $G\alpha$ protein (Hackenberg *et al.*, 2016).

Although plants have a limited number of G protein isoforms, G proteins play important roles in almost all aspects of biological

Article

A surface-receptor-coupled G protein regulates plant immunity through nuclear protein kinases

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SUMMARY

Plants employ cell-surface-localized pattern recognition receptors (PRRs) to recognize immunogenic patterns and activate defenses. How these receptors regulate immune signaling in the nucleus is not well understood. Our previous studies showed that BIK1, a central kinase associated with PRRs, phosphorylates a plant-specific G α protein called extra-large G protein 2 (XLG2) to positively regulate immunity. Here, we show that this phosphorylation promotes XLG2 nuclear translocation, which is essential for antibacterial immunity. XLG2 interacts with nuclear-localized MUT9-like kinases (MLKs) to regulate transcriptome programming. MLKs negatively regulate plant immunity in a kinase activity-dependent manner, whereas XLG2 promotes defense gene expression and antibacterial immunity likely by inhibiting MLK kinase activity. A C-terminal motif in MLKs is essential for the interaction with XLG2, and this motif is required for the XLG2-mediated defense activation. Together, our findings reveal a previously unknown pathway and mechanisms by which cell surface receptors regulate transcriptome during pathogen invasion.

INTRODUCTION

Plants employ cell-surface-localized pattern recognition receptors (PRRs) to sense microbe- or plant-derived molecular patterns and trigger a series of immune responses to defend against various microbial invasions (Couto and Zipfel, 2016; Tang et al., 2017). For instance, Arabidopsis receptor kinase (RK) FLS2 recognizes the bacterial flagellin epitope flg22 in the presence of the co-receptor BAK1 (Chinchilla et al., 2006; Sun et al., 2013). Similarly, Arabidopsis PRRs EFR, LYK5, and Pep receptors (PEPRs) recognize bacterial elongation factor Tu epitope elf18, fungal-derived cell-wall component chitin, and plant elicitor peptides (Peps), respectively (Zipfel et al., 2006; Cao et al., 2014; Krol et al., 2010). Downstream of PRRs, the central immune kinase BIK1 and its close homologs PBS1-like (PBL) kinases directly phosphorylate multiple immune components to activate immune responses (Zhang et al., 2010; Lu et al., 2010; Liang and Zhou, 2018). These include the nicotinamide adenine dinucleotide phosphate (NADPH) oxidase respiratory burst homolog D (RbohD)

responsible for the production of reactive oxygen species (ROS) (Li et al., 2014; Kadota et al., 2014), cyclic nucleotide gated channels (CNGC2 and CNGC4) and OSCA1.3 controlling calcium influx (Tian et al., 2019; Thor et al., 2020), mitogen-activated protein kinase kinase kinases MPKKK3, MPKKK5, and MEKK1 governing MAP kinase cascades (Bi et al., 2018), and heterotrimeric G protein subunit extra-large G protein 2 (XLG2) and regulator of G protein signaling 1 (RGS1) (Liang et al., 2016, 2018b). While these explain pattern-triggered ROS production, calcium flux, and activation of MAP kinase cascades, how heterotrimeric G proteins regulate defenses remains unclear.

Heterotrimeric G proteins composed of G α , G β , and G γ subunits are major signal transduction modules in eukaryotes (McCudden et al., 2005; Temple and Jones, 2007). Arabidopsis carry a single canonical G α subunit (GPA1), three extra-large G α proteins (XLG1–3), one G β subunit (AGB1), and three G γ subunits (AGG1–3) (Stateczny et al., 2016). In the resting state, G α proteins bind to GDP and form heterotrimers with G $\beta\gamma$. In the activated state, G α proteins exchange GDP for GTP, giving

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Extra-large G proteins regulate disease resistance by directly coupling to immune receptors in *Nicotiana benthamiana*

Yixin Li¹, Qian Zhang¹, Lijing Gong², Jun Kong², Xiaodan Wang¹, Guangyuan Xu¹, Xujun Chen¹, Daolong Dou^{1,3} and Xiangxiu Liang^{1,2*}

Abstract

Heterotrimeric G proteins, comprising G α , G β , and G γ subunits, are key regulators of eukaryotic intracellular signaling. Extra-large G (XLG) proteins are a subfamily of plant-specific G α proteins interacting with plasma membrane-localized receptors to regulate multiple biological processes. The *Nicotiana benthamiana* genome encodes seven XLG proteins, NbXLG1–7, whose functions in disease resistance and underlying mechanisms are unknown. In this study, we silenced all the seven genes and found that disease susceptibility was enhanced when both *NbXLG3* and *NbXLG5* or *NbXLG4* was silenced. Then, we generated *N. benthamiana* *xlg3xlg5* double- and *xlg4* single-mutant lines using the CRISPR-Cas9 approach. All the mutants showed reduced resistance to the bacterial pathogen *Pseudomonas syringae* pv. *tomato* DC3000, the fungal pathogen *Sclerotinia sclerotiorum*, and a series of oomycete pathogens, including *Phytophthora capsici*, *Phytophthora infestans*, and *Phytophthora parasitica*. We further demonstrated that NbXLG3/4/5 positively regulated microbial pattern-induced reactive oxygen species burst and defense gene expression by directly coupling to the tested plant immune receptors. In addition, we examined the role of NbXLG3/4/5 in abiotic stress tolerance and observed that NbXLG3 and NbXLG5 negatively regulated plant resistance to high-salt, mannitol, and PEG. Our study demonstrates the possible role of NbXLG3/4/5 in response to biotic and abiotic stresses and provides insights for the improvement of plant resistance to environmental changes.

Keywords: NbXLG, Immune response, Plant resistance, Abiotic stress

Background

The heterotrimeric G protein complex, composed of α , β , and γ subunits, is one of the most important signal transducers in eukaryotic cells (Pandey 2019). G proteins are key regulators of extracellular signal transduction. In animals and fungi, the G α subunit is directly coupled to seven-transmembrane G protein coupled receptors (GPCRs) that perceive extracellular signals through the ectodomains. GPCRs transmit these extracellular

signals to G α s, causing G α s to exchange GDP for GTP, resulting in the activation of G protein heterotrimers. An activated G α separates from G $\beta\gamma$ and they each function on their downstream targets (also known as G protein effectors) to transduce and amplify signals (Oldham and Hamm 2008). In plants, there is mounting evidence that G proteins are directly coupled to single-transmembrane receptor-like proteins (RLPs) and receptor kinases (RKs) to transduce extracellular signals to downstream effectors (Bommert et al. 2013; Choudhury and Pandey 2015; Liang et al. 2016; Yu et al. 2018; Zhao et al. 2022). Animals have a much larger number of G protein subunits that can form multiple heterotrimer combinations. For example, humans have 23 G α s, 5 G β s, and 12 G γ s.

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A pair of G-type lectin receptor-like kinases modulates nlp20-mediated immune responses by coupling to the RLP23 receptor complex

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ABSTRACT

Plant cells recognize microbial patterns with the plasma-membrane-localized pattern-recognition receptors consisting mainly of receptor kinases (RKs) and receptor-like proteins (RLPs). RKs, such as bacterial flagellin receptor FLS2, and their downstream signaling components have been studied extensively. However, newly discovered regulatory components of RLP-mediated immune signaling, such as the nlp20 receptor RLP23, await identification. Unlike RKs, RLPs lack a cytoplasmic kinase domain, instead recruiting the receptor-like kinases (RLKs) BAK1 and SOBIR1. SOBIR1 specifically works as an adapter for RLP-mediated immunity. To identify new regulators of RLP-mediated signaling, we looked for SOBIR1-binding

proteins (SBPs) in *Arabidopsis thaliana* using protein immunoprecipitation and mass spectrometry, identifying two G-type lectin RLKs, SBP1 and SBP2, that physically interacted with SOBIR1. SBP1 and SBP2 showed high sequence similarity, were tandemly repeated on chromosome 4, and also interacted with both RLP23 and BAK1. *sbp1 sbp2* double mutants obtained via CRISPR-Cas9 gene editing showed severely impaired nlp20-induced reactive oxygen species burst, mitogen-activated protein kinase (MAPK) activation, and defense gene expression, but normal flg22-induced immune responses. We showed that SBP1 regulated nlp20-induced immunity in a kinase activity-independent manner. Furthermore, the nlp20-induced the RLP23–BAK1 interaction, although not the flg22-induced FLS2–BAK1 interaction, was significantly reduced in *sbp1 sbp2*. This study identified SBPs as new regulatory components in RLP23 receptor complex that may specifically modulate RLP23-mediated immunity by positively regulating the interaction between the RLP23 receptor and the BAK1 co-receptor.

Keywords: immune responses, pattern-recognition receptors, receptor-like proteins, SBPs, SOBIR1

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INTRODUCTION

Plants are threatened by various microbial pathogens. To defend themselves from microbial pathogen invasions, plants have evolved a multilayered innate immune system. Successful

recognition of microbial patterns is a key step in the initiation of plant immune responses. Microbial patterns are conserved molecular features of microorganisms that are recognized by cell-surface-localized pattern-recognition receptors (PRRs) of plants (Couto and Zipfel, 2016; Tang et al., 2017). PRRs can

CPR5 positively regulates pattern-triggered immunity via a mediator protein

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Miaomiao Ma



Xiangxiu Liang

SUMMARY

Plant cells possess a two-layered immune system consisting of pattern-triggered immunity (PTI) and effector-triggered immunity (ETI), mediated by cell surface pattern-recognition receptors and intracellular nucleotide-binding leucine-rich repeat

receptors (NLRs), respectively. The CONSTITUTIVE EXPRESSION OF PR GENES 5 (CPR5) nuclear pore complex protein negatively regulates ETI, including ETI-associated hypersensitive response. Here, we show that CPR5 is essential for the activation of various PTI responses in *Arabidopsis*, such as resistance to the non-adapted bacterium *Pseudomonas syringae* pv. *tomato* DC3000 *hrcC*. In a forward-genetic screen for suppressors of *cpr5*, we identified the mediator protein MED4. Mutation of *MED4* in *cpr5* greatly restored the defective PTI of *cpr5*. Our findings reveal that CPR5 plays opposite roles in regulating PTI and ETI, and genetically regulates PTI via MED4.

Keywords: CPR5, MED4, plant immunity, PTI

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INTRODUCTION

Plants employ pattern-recognition receptors (PRRs) to recognize pathogen/microbe-associated molecular patterns (PAMPs/MAMPs) or damage-associated molecular patterns (DAMPs) to activate pattern-triggered immunity (PTI) (DeFalco and Zipfel, 2021). For instance, in the presence of the co-receptor BAK1, FLS2 recognizes bacterial flagellin (or the flg22 epitope) in *Arabidopsis thaliana* (Chinchilla et al., 2007). Similarly, LYK4 or LYK5 forms a complex with CERK1 to recognize chitin derived from fungal cell walls (Miya et al., 2007; Cao et al., 2014). Plant-derived plant-elicitor peptides


(Peps) are perceived by the receptors PEPR1 and PEPR2, together with their co-receptor BAK1 (Yamaguchi et al., 2010). PRRs transmit signals to downstream signaling components and induce a series of immune responses, including the transient production of reactive oxygen species (ROS), activation of the mitogen-activated protein kinase (MAPK) cascade, and transcriptome reprogramming (DeFalco and Zipfel, 2021). PTI confers moderate resistance to most microbes, including adapted and non-adapted pathogens, at relatively low growth costs. Successful pathogens can evade host immunity by secreting effectors into the host cells that suppress plant immune signaling (Wang et al., 2022). In turn,

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A pair of soybean malectin-like domain-containing receptor-like kinases jointly regulate pattern-triggered immunity by forming hetero-oligomers

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Abstract

Plant cells perceive pathogen invasion by recognizing microbial patterns using plasma-membrane-localized pattern-recognition receptors (PRRs) to initiate pattern-triggered immunity (PTI), which confers a moderate immunity to most microbes. For instance, the PRR FLS2 (FLAGELLIN SENSING 2) recognizes bacterial flagellin in the presence of the co-receptor BAK1 and activates a series of PTI responses, such as reactive oxygen species (ROS) burst and mitogen-activated protein kinase (MAPK) activation. We previously showed that soybean malectin/malectin-like domain-containing receptor-like kinase (MRLK) protein GmLMM1 negatively regulates PTI by suppressing FLS2-BAK1 interaction. GmLMM1 replicates in tandem with five other GmMRLKs on chromosome 13. Here, we show that GmMRLK32, the closest homolog to GmLMM1 among the tandem genes of GmMRLKs, negatively regulates PTI and disease resistance against bacterial and oomycete pathogens. The *Gmmrlk32* mutant showed enhanced flg22-induced ROS burst and MAPK activation. We revealed that GmMRLK32 interacts with GmFLS2 and GmBAK1, and suppresses flg22-induced GmFLS2-GmBAK1 dimerization in a manner similar to that of GmLMM1. We further showed that GmMRLK32 specifically interacts with GmLMM1 to regulate PTI. In *Nicotiana benthamiana* plants, co-expression of GmMRLK32 and GmLMM1 showed a stronger PTI inhibitory effect on PTI activation than expression of GmMRLK32 or GmLMM1 alone. We uncovered a novel mechanism by which GmMRLK32 and GmLMM1 coordinately regulate PTI by forming hetero-oligomer.

Keywords Soybean, Malectin/malectin-like domain-containing receptor-like kinases, Pattern-recognition receptors (PRRs), Pattern-triggered immunity (PTI)

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RESEARCH

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Joint application of plant immunity-inducing elicitors and fungicides to control *Phytophthora* diseases

Rubin Chen¹, Dicheng Ma¹, Yazhou Bao^{1,2}, Weijie Wang¹, Dandan Du¹, Xujun Chen¹, Daolong Dou^{1,2*} and Xiangxiu Liang^{1,3*} 

Abstract

Phytophthora are destructive plant pathogens that pose a serious threat to crop production. Traditional control methods rely heavily on chemical fungicides, which are harmful to the environment and human health. Currently, effective green prevention and control methods for *Phytophthora* pathogens are lacking. Plants rely primarily on their innate immune system to resist pathogens. Plant cells perceive pathogen invasion and activate immune responses by recognizing specific pathogen-derived molecules, called elicitors, which mainly include pathogen-associated molecular patterns (PAMPs) and microbial effector proteins. PAMPs, which are conserved molecular features of microbes and recognized by plant cell surface-localized pattern-recognition receptors (PRRs), activate mild and broad-spectrum disease resistance. However, there are few reports on elicitor proteins that induce broad resistance against *Phytophthora* pathogens. In this study, we identified BcIEB1, a fungal-derived PAMP, which activated plant immune responses in a BAK1- and SOBIR1-dependent manner. BcIEB1 could induce plant resistance to various *Phytophthora* pathogens, including *P. capsici*, *P. infestans*, and *P. parasitica*. We further found that the combination of lower concentrations of BcIEB1 with fungicides, such as pyraclostrobin, azoxystrobin, and metalaxyl-M, could enhance the effect on *Phytophthora* disease control while reducing the dependence on fungicides, thereby reducing environmental pollution. This study identified a novel, less toxic strategy for controlling *Phytophthora* diseases.

Keywords *Phytophthora* diseases, Elicitor, PAMP, Plant immunity, Fungicide

Background

Phytophthora, a unique genus of the Oomycetes, is morphologically similar to filamentous fungi; however, they differ in many aspects, such as cell wall composition, biochemical metabolism, and reproductive methods (Jiang and Tyler 2012). *Phytophthora* species are highly destructive plant pathogens that significantly threaten crop production. With over 100 members reported, pathogenic *Phytophthora* species are responsible for diseases such as late blight in potatoes, which causes an estimated \$6 billion in agricultural losses globally (Haverkort et al. 2008). For example, *P. capsici* is a highly damaging oomycete pathogen with a wide host range, infecting Solanaceous plants such as peppers and tomatoes, legumes, and

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Metformin blocks BIK1-mediated CPK28 phosphorylation and enhances plant immunity

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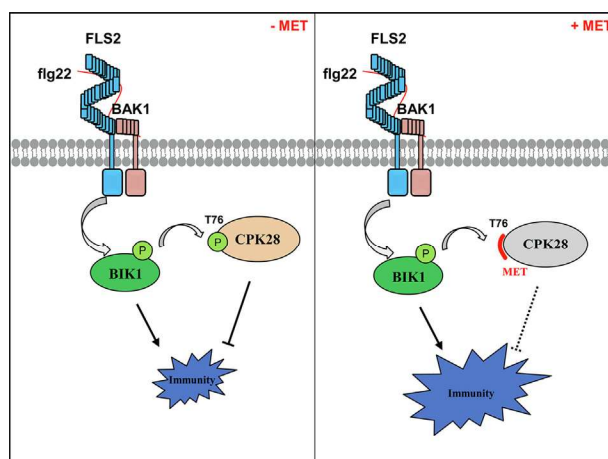
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HIGHLIGHTS

- MET and its derivatives enhance plant resistance by inducing and strengthening immune responses.
- MET targets CPK28 at T76 and inhibits its interaction with BIK1.
- MET masks T76 to prevent its phosphorylation by BIK1 and suppresses CPK28 function.
- Our study identifies a novel broad-spectrum chemical plant immunity inducer family and elucidates a mechanism that can serve as a starting point for the development of novel agrochemicals.

GRAPHICAL ABSTRACT



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ABSTRACT

Introduction: Metformin (MET), derived from *Galega officinalis*, stands as the primary first-line medication for the treatment of type 2 diabetes (T2D). Despite its well-documented benefits in mammalian cellular processes, its functions and underlying mechanisms in plants remain unclear.

Objectives: This study aimed to elucidate MET's role in inducing plant immunity and investigate the associated mechanisms.

Methods: To investigate the impact of MET on enhancing plant immune responses, we conducted assays measuring defense gene expression, reactive oxygen species (ROS) accumulation, mitogen-activated protein kinase (MAPK) phosphorylation, and pathogen infection. Additionally, surface plasmon resonance (SPR) and microscale thermophoresis (MST) techniques were employed to identify MET targets. Protein-protein interactions were analyzed using a luciferase complementation assay and a co-immunoprecipitation assay.

Results: Our findings revealed that MET boosts plant disease resistance by activating MAPKs, upregulating the expression of downstream defense genes, and fortifying the ROS burst. CALCIUM-DEPENDENT PROTEIN KINASE 28 (CPK28) was identified as a target of MET. It inhibited the interaction between

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Perspective

Phosphorylation-dependent regulation of plant heterotrimeric G proteins: From activation to downstream signaling

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Heterotrimeric G proteins (G proteins) composed of $G\alpha$, $G\beta$, and $G\gamma$ subunits are universal signaling modules in eukaryotes. In plants, G proteins regulate almost all aspects of biological processes, including plant growth, development, responses to abiotic stresses and hormones, and plant–microbe interactions [1]. *Arabidopsis* and rice possess four and five $G\alpha$ s, one $G\beta$, and three and five $G\gamma$ subunits, respectively [1,2]. Notably, there are subfamilies of plant-specific $G\alpha$ and $G\gamma$ proteins, the extra-large G (XLG) proteins and type C $G\gamma$ proteins, which are widespread in higher plants. XLGs contain a C-terminal $G\alpha$ -like domain and an N-terminal extension. Plant $G\gamma$ proteins can be divided into three subfamilies: type A $G\gamma$ subunits possess a conserved prenylation CaaX motif, whereas type B subunits lack it, and type C $G\gamma$ subunits contain a C-terminal cysteine-rich domain [2].

In the animal model, the off/on state of G proteins is mainly determined by the GDP- or GTP-bound state of $G\alpha$. The activated $G\alpha$ and $G\beta\gamma$ transmit downstream signaling through their targets (also known as G protein effectors) [1]. Animal G proteins are coupled to seven-transmembrane G protein-coupled receptors (7-TM GPCRs) and are activated by the guanine nucleotide exchange factor (GEF) activity of GPCRs [1,2]. However, no functional GPCRs with GEF activities have been identified in plants. For a long time, how plant G proteins receive, are activated by, and propagate extracellular signals remains largely elusive.

Plant G proteins couple to single transmembrane RLKs or RLPs. In animals, heterotrimeric G proteins directly interact with the intracellular domain of GPCRs, the major type of receptors found on animal cell surfaces, to receive extracellular signals [1,2]. However, plant G proteins are directly coupled to single transmembrane receptor-like kinases (RLKs) or receptor-like proteins (RLPs) to perceive extracellular signals and interact with a number of key kinase families to transduce downstream signals. Therefore, the phosphorylation modification plays an essential role in plant G protein signaling.

RLKs and RLPs are the major receptors on plant cell surfaces and are involved in the perception and transduction of various signals through phosphorylation [3]. RLKs contain an intracellular kinase domain and an extracellular ligand-binding domain. RLPs structurally resemble RLKs, but lack an intracellular kinase domain [3]. Increasing evidence for direct interaction between G proteins and RLKs/RLPs was reported. It was shown that the maize $G\alpha$ protein CT2 interacts with FEA2, an RLP receptor that mediates CLV3 peptide hormone-mediated signaling, to regulate shoot apical meristem (SAM) development [4]. In soybean, the $G\alpha$ subunit was reported to directly interact with the RLK protein NFR1, the receptor for Nod factor, to regulate nodule development [5]. *Arabidopsis* G protein subunits, GPA1, XLGs, AGB1, and AGG1/2 directly interact with FLS2, an RLK receptor that recognizes bacterial flagellin, to regulate plant immunity [6]. *Arabidopsis* $G\beta\gamma$ was reported to interact with BR receptor BRI1 and co-receptor BAK1 to regulate sugar-responsive growth and development [7]. Taken together, these reports demonstrate that plant G proteins perceive extracellular signals through plasma-membrane localized RLKs or RLPs. The large number of RLKs/RLPs in plants suggests that signal discrimination through G proteins is likely to be achieved by RLKs/RLPs.

RLK or RLP receptor-mediated phosphorylation of RGS1. In animal model, when $G\alpha$ binds with GDP, it directly couples to the intracellular domain of GPCRs and maintains a resting state by forming a heterotrimer with $G\beta\gamma$. When GPCRs bind extracellular ligands, conformational changes occur in the intracellular GEF domain, and $G\alpha$ exchanges GDP for GTP. Next, the GTP-bound $G\alpha$ dissociates from the $G\beta\gamma$ dimer, and each transduces the signal to their respective downstream effectors [1]. Unlike animal G proteins, plant $G\alpha$ subunits spontaneously bind GTP and exhibit auto-activation activity *in vitro* [8]. It is unclear how can self-activating plant $G\alpha$ proteins maintain in the inactive GDP-bound state *in vivo*. *Arabidopsis* RGS1 (Regulator of G Protein Signaling 1) has an N-terminal seven-transmembrane domain and a C-terminal RGS box domain, with the GAP (GTP-Accelerating Protein) activity to promote $G\alpha$ hydrolysis of GTP to GDP *in vitro* [9]. In the research on G protein-mediated sugar signaling, a study showed that phosphorylation of the RGS1 C-terminal tail with no lysine kinase 8

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The OXIDATIVE SIGNAL-INDUCIBLE1 kinase regulates plant immunity by linking microbial pattern-induced reactive oxygen species burst to MAP kinase activation

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Abstract

Plant cell surface-localized pattern recognition receptors (PRRs) recognize microbial patterns and activate pattern-triggered immunity (PTI). Typical PTI responses include reactive oxygen species (ROS) burst controlled by the NADPH oxidase RESPIRATORY BURST OXIDASE HOMOLOG D (RbohD) and activation of the MAP kinase (MAPK) cascade composed of MAPKKK3/5–MKK4/5–MPK3/6. However, the mechanisms through which PRRs regulate and coordinate these immune responses are not fully understood. Here, we showed that *Arabidopsis thaliana* OXIDATIVE SIGNAL-INDUCIBLE1 (OXI1), a kinase known to be activated by ROS, is involved in the LYK5–CERK1 receptor complex, which recognizes fungal cell wall-derived chitin. The *oxi1* mutant exhibits enhanced susceptibility to various pathogens and reduced chitin-induced MAPK activation and ROS burst. We showed that chitin induces the phosphorylation of OXI1 in an RbohD-dependent manner. H₂O₂ and chitin treatment causes the oxidation of OXI1 at Cys104 and Cys205, which is essential for the kinase activity of OXI1. These oxidation sites are required for chitin-induced MAPK activation and disease resistance. Activated OXI1 directly phosphorylates MAPKKK5 to regulate MAPK activation. Additionally, OXI1 phosphorylates RbohD, suggesting that it may activate RbohD to promote ROS burst to further enhance the long-term MAPK activation. Together, our findings reveal a pathway linking PRR-mediated ROS production to MAPK activation through OXI1.

Introduction

Plants rely primarily on their innate immune system to defend against microbial pathogen invasion. Plant cell surface-localized pattern recognition receptors (PRRs) recognize conserved molecular patterns, such as fungal cell wall-derived chitin and bacterial flagellin, to sense pathogen invasion and activate pattern-triggered immunity (PTI; DeFalco and Zipfel 2021). PTI plays a key role in plant basal resistance and confers broad-spectrum resistance to most microbes. Successful recognition of microbial patterns by PRRs and their coreceptors is the key step for the initiation of PTI. PRRs consist of receptor-like kinases (RLKs) and receptor-like proteins (RLPs; Tang et al. 2017). BRASSINOSTEROID INSENSITIVE1-ASSOCIATED KINASE1 (BAK1) is known to serve as a coreceptor for most RLK and RLP receptors that have an extracellular leucine-rich repeat (LRR) domain (Ma et al. 2016). CHITIN ELICITOR RECEPTOR KINASE1 (CERK1) functions as a coreceptor for many LysM-type RLK receptors (Yang et al. 2022). For example, the *Arabidopsis* (*Arabidopsis thaliana*) LRR–RLK receptor FLAGELLIN SENSITIVE2 (FLS2) recognizes flagellin (or the flg22 epitope) in the

presence of BAK1 (Chinchilla et al. 2007). LysM–RLK protein LYSIN MOTIF RECEPTOR KINASE4 (LYK4) or LYK5 forms a complex with CERK1 to recognize chitin (Cao et al. 2014). The RLP receptor RECEPTOR-LIKE PROTEIN23 (RLP23) constitutively interacts with SUPPRESSOR OF BIR1 1 and rapidly recruits BAK1 to recognize nlp20 peptide (Albert et al. 2015). PRRs also form complexes with certain key regulatory components, such as receptor-like cytoplasmic kinase (RLCK) protein BOTRYTIS-INDUCED KINASE1 (BIK1; Lu et al. 2010; Zhang et al. 2010), malectin-like RLK proteins FERONIA and ANXUR1 (Mang et al. 2017; Stegmann et al. 2017), NADPH oxidase RESPIRATORY BURST OXIDASE HOMOLOG D (RbohD; Kadota et al. 2014; Li et al. 2014), and heteromeric G protein subunit EXTRA-LARGE G PROTEIN2 (XLG2; Liang et al. 2016), to achieve immune signal transduction and regulation (DeFalco and Zipfel 2021). Upon perception of microbes by PRRs, PRR complexes initiate a series of immune responses, including transient influx of calcium, reactive oxygen species (ROS) burst, activation of MAP kinase (MAPK) cascades, and transcriptional reprogramming (Couto and Zipfel 2016).

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荣誉证书

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项目名称：微生物激发子蛋白诱导药用植物紫锥菊活性成分积累的功能和机制研究

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