

植物模式识别受体与先天免疫

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摘要: 为争夺各自的生存资源和空间, 自然万物之间既相互联系又相互战斗。植物同病原微生物以及共生微生物之间也在长期的相互斗争中一起协同进化, 最终维持在一个相对稳定的状态。从农耕文明发展至今, 植物病害造成的损失不计其数, 所以对植物与病原微生物, 以及共生微生物之间关系的阐释和植物抗病信号途径中各成员功能的揭示, 对未来农业的可持续发展将起到极其重要的作用。近年来, 基于分子生物学、遗传学和生理生化检测技术的飞速发展, 研究者对植物抗病信号途径, 尤其是植物模式识别受体与先天免疫的关系有了一些初步认知, 对深入认识植物同微生物之间协同进化的关系奠定了基础。本文综述了近年来植物模式识别受体识别外源或内源免疫触发因子从而触发植物先天免疫信号的最新研究进展, 以期阐释植物同微生物之间的关系提供理论依据, 并为培育符合社会发展需求的抗病作物提供一定指导。

关键词: 模式识别受体; 类受体激酶; 类受体蛋白; 病原微生物; 先天免疫

Pattern recognition receptors and plant innate immunity

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Abstract: In order to fight for their own living resources and space, natural things are interrelated and exclusionary with each other. In a long struggle, plants co-evolved with beneficial or pathogenic microorganisms, and maintain a relatively stable state in the end. Since the initiation of agricultural civilization, plant diseases have caused untold losses. If we clearly explain the relationship between plants and beneficial or pathogenic microorganisms and know the functions of each member in the plant disease resistance signal pathways, it will be beneficial to the sustainable development of agriculture in the future. In recent years, based on the development of molecular biology, genetics, physiological and biochemical detection techniques, researchers have gained some preliminary understanding of plant disease resistance, especially the relationship between plant pattern recognition receptors and innate immunity, this laying the foundation for a deeper understanding of the co-evolutionary relationship between plants and microorganisms. In this review, we discussed the recent advances in plant pattern recognition receptors and exogenous or endogenous elicitor. Look forward to providing a theoretical basis to explain the relationship be-

收稿 2020-09-11 修定 2020-12-06

资助 国家自然科学基金面上项目(31860113)和兰州大学细胞活动与逆境适应教育部重点实验室开放基金(2019-kb05和2017-kb05)。

tween plants and microorganisms, and provide guidance to cultivation of disease-resistant crops which meet the needs of social development.

Key words: pattern recognition receptors; receptor-like protein kinases; receptor-like protein; innate immunity

“咬定青山不放松，立根原在破岩中。千磨万击还坚劲，任尔东西南北风”，从我国清代文学家郑燮的诗句中足以看到植物在历经各种逆境胁迫时所展现出的顽强生命力。经现代科学家的研究发现，植物之所以能够适应外界复杂的非生物逆境胁迫，主要得力于定位于细胞膜上的众多类受体蛋白对外界胁迫信号的感知，然后经过一系列复杂而精细的信号转导，使植物可以对多变的外界环境做出正确响应，以维持其生存和发展。同样，这些受体蛋白也可以使植物在遭受各种生物胁迫的刺激，如病原微生物等的危害时，启动自身免疫防御系统，使植物在一定程度上抵御外源侵害。研究显示，全球主要粮食作物每年因病虫害造成的损失约占总产量的20%~30%，导致全球经济危机和粮食安全问题的进一步加剧(Savary等2019)，所以对植物免疫防御信号转导网络的研究一直是植物学研究领域的热点之一。

在植物与病原微生物长期协同进化的过程中，植物形成了两层独特的免疫防御体系来应对病原微生物的侵害(Jones和Dangl 2006)，第一层免疫防御体系依赖于细胞膜上的模式识别受体(pattern

recognition receptors, PRRs)，通过识别一些具有特殊保守基序的有害信号分子，如外源微生物相关分子模式(microbe-associated molecular pattern, MAMP)或内源损伤相关分子模式(damage-associated molecular pattern, DAMP)而触发的先天免疫反应，我们称之为模式识别受体触发的免疫(PRR-triggered immunity, PTI) (Boller和Felix 2009)。目前研究认为模式识别受体包括类受体蛋白激酶(receptor-like protein kinases, RLK)和类受体蛋白(receptor-like proteins, RLPs)两类(Macho 和 Zipfel 2014; Wu 和 Zhou 2013)。RLK是位于细胞膜上的一类单次跨膜蛋白，由可与MAMP或DAMP结合的胞外结构域、跨膜结构域以及胞内激酶结构域组成(Shiu和Bleecker 2001)。RLK是植物体内数量最为庞大的一类受体蛋白，由于其胞外结构域的结构差异，使其可与不同的配体相结合以调控植物特定的信号转导途径，进而协调整个植物的生长发育过程(Jose等2020)。RLP的蛋白结构与RLK类似，但缺少胞内激酶结构域，所以RLP通常与RLK或其他蛋白形成受体复合体共同介导PTI信号的向下传递(Wang等2008) (图1)。然而伴随着病原微生物的协

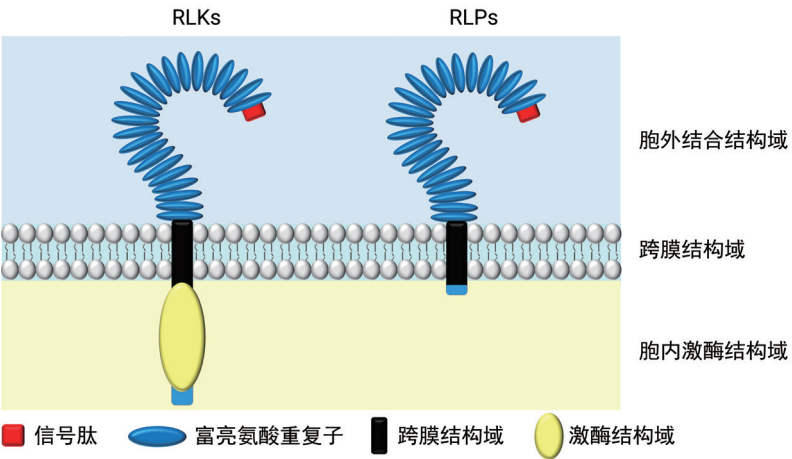


图1 类受体蛋白激酶和类受体蛋白的蛋白结构

Fig. 1 The protein structures of receptor-like protein kinase and receptor-like protein

同进化, 其衍生出的众多效应蛋白(effectors)可直接或间接攻击PTI信号途径的关键信号元件, 造成PTI信号的抑制, 从而增强病原微生物侵染植物的能力, 导致植物效应因子触发易感性(effector-triggered susceptibility, ETS)的产生(Deller等2011)。因此为了克服病原微生物对植物的侵害, 植物又进化出了核苷酸结合富亮氨酸重复受体[nucleotide-binding (NB) leucine-rich repeat (LRR) domain receptors, NLRs], 可通过特异性识别并结合效应蛋白, 而激活第二层效应蛋白触发的免疫(effector-triggered immunity, ETI) (Boller和Felix 2009)。相比于PTI, ETI介导的免疫反应更为强烈, 通常伴随着局部细胞的程序性死亡, 即超敏反应(hypersensitive response, HR), 可将病原微生物“饿死”在局部空间, 防止对临近细胞的进一步侵染(Katagiri和Tsuda 2010)。综上所述, PTI和ETI调控的植物免疫抗性此消彼长, 形成了典型的“Z”字型模式, 无论在细胞内还是在细胞外均时刻监控着是否存在有害信号分子, 以调控植物的免疫抗性维持其正常生长发育(Cook等2015; Gust等2017; Jones和Dangl 2006)。本文基于植物同病原微生物的协同进化过程, 对PRR的功能以及其介导的下游免疫信号进行概述。

1 PRRs与真菌的识别

植物在遭受真菌侵染时, 往往会导致植物细胞和组织的坏死腐烂以及植株的萎蔫。但是不同的植物对同一真菌的抗性反应却千差万别, 说明某些特定植物在长期进化中形成了可以识别真菌的免疫防御系统。由于几丁质是真菌细胞壁的主要组成成分, 由N-乙酰氨基葡萄糖聚合而成, 且该类物质在植物体内并未发现(Kaku等2006)。研究者通过筛选对几丁质响应发生变化的遗传突变体, 发现胞外含有三个LysM结构域的LRK、CERK1, 就是几丁质的PRR (Miya等2007), 因为细菌细胞壁的降解酶以及酵母和低等植物的几丁质酶均含有典型的LysM结构域, 所以暗示着CERK1负责识别并结合外源几丁质而触发植物下游免疫信号(Wan等2008), 通过调控植物激素的动态变化、细胞内离子流的变化、丝裂原活化蛋白激酶(mitogen-ac-

tivated protein kinase, MAPK)的顺序性激活、活性氧的爆发、抗菌类物质的合成, 赋予植物对真菌的抗性免疫(Chinchilla等2007)。

基于对CERK1的蛋白结构解析, 研究者证实拟南芥(*Arabidopsis thaliana*)中CERK1为几丁质的受体, 同时由7~8个N-乙酰氨基葡萄糖聚合而成的高聚体几丁质可诱导活性形式CERK1同源二聚体的形成, 而由4~5个N-乙酰氨基葡萄糖聚合而成的低聚体几丁质虽然也可以被CERK1中的第2个LysM结构域所识别, 但却不能诱导形成具有活性的CERK1同源二聚体(Liu等2012b; Petutschnig等2010)。随后有研究显示CERK1其实对几丁质的结合能力较低, 而它的同源蛋白LYK5则表现出更高的几丁质结合能力, 而且LYK5和LYK4 (LYK5的同源基因)的缺失突变体对几丁质的敏感性已经显著降低, 所以目前认为LYK5是主要的几丁质受体, 与CERK1共同介导几丁质触发的下游免疫信号(Cao等2014; Wan等2012)。在水稻(*Oryza sativa*)中, 虽然CERK1也参与几丁质介导的免疫反应, 但主要通过同样拥有LysM胞外结构域的受体蛋白OsCEBiP直接感知外源几丁质的刺激(Kaku等2006; Shimizu等2010)。蛋白结构显示OsCEBiP也具有3个串联的LysM结构域, 且和拟南芥的CERK1一样, 仅受体复合体中第2个LysM结构域参与几丁质的识别(Liu等2016)。

由于CERK1并不能直接识别N-乙酰氨基葡萄糖高度聚合的几丁质, 所以植物细胞在遭受真菌侵染时往往会自主产生几丁质酶, 通过消化真菌细胞壁中的几丁质多糖, 产生可被CERK1顺利识别的MAMP而激活下游免疫信号(Collinge等1993; Kombrink等2011; Liu等2014)。但有研究发现, 病原菌*Verticillium dahlia*为了逃避几丁质酶对其细胞壁多糖的降解, 可分泌一种丝氨酸蛋白酶(VdS-SEP1), 通过水解几丁质酶Chi28而抑制下游免疫信号的激活(Han等2019), 同时真菌细胞分泌的几丁质去乙酰化酶也可使几丁质寡糖去乙酰化而变为不能被CERK1识别的壳寡糖(Ye等2020)。所以在植物同病原微生物相互斗争的共进化过程中, 病原菌要主动逃避几丁质酶对其细胞壁的降解, 而植物在进化中又需要再次保障几丁质酶的正常

酶活。因此棉花细胞中的CRR1 (CYS-RICH REPEAT PROTEIN 1)就可保护Chi28不被蛋白酶水解(Han等2019),且在共进化过程中,植物的CERK1虽然不能识别壳寡糖,但其可被其他未知受体所识别,通过促进保卫细胞的死亡以抵抗真菌的入侵(Ye等2020)。

研究发现,除了真菌特有的几丁质,其他的一些真菌MAMP也可被植物特定的PRRs所识别而触发下游免疫响应。如番茄(*Solanum lycopersicum*)的LRR-RLPs Eix2可识别真菌源的木聚糖酶(ethylene-inducing xylanase, EIX),并通过与Eix1和BAK1 (BRI1-ASSOCIATED RECEPTOR KINASE 1)的相互作用激活植物的抗病反应(Bar等2010; Ron和Avni 2004)。在拟南芥中,真菌的内聚半乳糖醛酸酶则可被LRR-RLP42 (RBGP1)所识别,并依赖于SOBIR1 (SUPPRESSOR OF BIR1)激活植物抗性反应(Poinsot等2003; Zhang等2014)。但目前对真菌木聚糖酶和内聚半乳糖醛酸酶的作用机理和下游信号元件的研究还相对较少,同时在信号识别初期,植物是否进化出应对木聚糖酶和内聚半乳糖醛酸酶侵害的蛋白分子目前也都一无所知。对于益生微生物根瘤菌,研究者发现同样拥有LysM结构域的受体蛋白NFR1还会通过识别根瘤菌分泌的结瘤因子(Nod factors)使豆科植物与根瘤菌相互共生(Broghammer等2012; Feng等2019; Kawaharada等2015; Madsen等2003)。最近研究者发现植物LysM受体胞外结构域的特异性决定了植物对几丁质或Nod因子的特异性识别,初步阐释了植物精确调控自身免疫防御反应而区别对待益生菌的分子机理,也为非豆科植物的结瘤固氮提供了可能(Bozsoki等2020)。

2 PRRs与细菌的识别

细菌与植物的关系研究开始的相对较早,FLS2 (FLAGELLIN-SENSITIVE 2)是植物体内第一个被鉴定发现的LRR-RLK类PRR (Gómez-Gómez等2001),通过特异性识别并结合细菌鞭毛蛋白N端含有22个氨基酸残基的保守蛋白多肽flg22而激活植物免疫响应(Bauer等2001; Chinchilla等2006; Meindl等2000)。因为鞭毛蛋白是细菌运动的重要

器官,所以FLS2仅需要识别其N端高度保守的多肽序列即可对众多的病原微生物产生广谱抗性。通过分析FLS2与flg22的蛋白结构,研究者发现flg22伸展地结合在FLS2胞外区螺线管状凹面上,起到连接FLS2和共受体BAK1胞外区的作用,使之成为具有活性功能的异源受体复合体而介导下游信号传递(Sun等2013)。而且FLS2对鞭毛蛋白的识别在不同的植物物种间还具有不同的配体特异性,如番茄的FLS2仅识别含有15个氨基酸残基的蛋白多肽flg15,而在拟南芥和烟草(*Nicotiana tabacum*)中flg15并不能有效地激发植物的PTI响应(Robatzek等2007),同时番茄通过自然变异形成的另一个LRR-RLK FLS3,则用以识别细菌的鞭毛蛋白flgII-28,说明在共进化过程中植物进化出多个不同的PRRs,通过不同的识别方式高效地识别同一个病原微生物蛋白而增强其抗性(Hind等2016)。

但植物对细菌鞭毛蛋白的识别也同样并非一蹴而就,因为细菌鞭毛蛋白往往被糖基化修饰,且高度聚集成复杂蛋白结构,因此具有免疫活性的保守多肽并非暴露于表面而被植物直接识别。所以为了克服识别障碍,植物同样在进化中形成了一种存在于胞外的 β -半乳糖苷酶BGAL1,其特异性地水解被特定糖基化修饰的鞭毛蛋白,从而将保守多肽释放出来帮助受体识别(Buscaill等2019)。基于此,某些病原微生物如*Pseudomonas syringae* pv. *syringae* (Psy B728a)又进化出其他类型糖基化修饰的鞭毛蛋白,以逃避BGAL1的识别水解(Buscaill等2019; Yamamoto等2011)。当然,植物与病原微生物之间的这种博弈并非止步于此,伴随着它们相互的共进化,还有很多未解之谜等待我们去探索发现。

在水稻中,LRR-RLK XA21可识别*Xanthomonas oryzae* pv. *oryzae* (Xoo)分泌的蛋白多肽Ax21,从而介导植物抗病反应,但拟南芥FLS2的突变体却对Ax21的敏感性显著降低,暗示着FLS2除了识别细菌鞭毛蛋白还可能识别其他配体(Danna等2011)。同时研究者在拟南芥中异源表达水稻FLS2,转基因植物则丧失了对Xoo的感知,说明不同的植物种群对鞭毛蛋白的感知还存在一定的差异性(Takai等2008; Wang等2015)。

当研究者用鞭毛蛋白缺失的大肠杆菌GI826提取物处理拟南芥细胞时,发现其依然存在免疫响应,表明除了鞭毛蛋白还存在其他的MAMP可激活植物免疫。经鉴定这类MAMP正是原核生物所特有的转录延伸因子Tu (elongation factor Tu, EF-Tu),其N端经乙酰化修饰,前18个氨基酸残基elf18就可激活植物的免疫抗病反应(Kunze等2004)。同flg22类似,elf18也被包裹在EF-Tu复杂的蛋白结构中,但植物通过怎样的方式将elf18从复杂蛋白结构中暴露出来进行识别目前还一无所知。经反向遗传学筛选,研究者发现elf18的受体为同属于LRR-RLK的EFR (Zipfel等2006)。但烟草几乎丧失了感知EF-Tu的能力,除非将拟南芥EFR进行异源表达才能重新赋予转基因烟草感知EF-Tu的能力(Lacombe等2010; Zipfel等2006)。因此从进化的角度来看,EFR似乎进化时间较晚,因为只有芸苔科或豆科植物才能感知EF-Tu (Böhm等2014),说明植物的PRRs在介导PTI响应中是一类可替换的“模块”,且病原微生物与宿主植物的博弈就依赖于其特有的PRRs,所以也为未来新型抗病作物的培育提供了方向和可能。

肽聚糖(peptidoglycans, PGNs)是大多数细菌细胞壁的主要组成成分,在细菌生长过程中由于细胞壁重塑而被释放,它也是一种可触发植物免疫响应的信号分子,在拟南芥中被同样含有LysM域的一类受体蛋白LYM1和LYM3所识别,并与CERK1协同作用共同介导下游免疫信号(Willmann等2011; Zhang等2009)。但有意思的是拟南芥CERK1并不能结合PGNs,同样LYM1和LYM3也不能识别几丁质(Iizasa等2010; Liu等2012b; Petutschnig等2010),而在水稻中,LYM3的同源基因LYP4和LYP6不仅可以结合PGNs,还可以识别几丁质介导植物抗性反应(Liu等2012a)。

脂多糖(lipopolysaccharide, LPS)同样是革兰氏阴性细菌细胞外壁的组成成分,也是植物或动物PRR可感知的一类MAMP (Kagan 2017; Ranf 2016)。在拟南芥中SD1-29 (S-domain-1 RLK LORE)被认为是感知LPS的受体,但目前发现LORE对LPS的识别仅局限于十字花科植物,同时LORE貌似并不参与大肠杆菌中LPS的识别,暗示着植物中可能还

存在着不同的LPS受体(Ranf等2015)。随着人们对植物和病原微生物的深入研究,越来越多新的MAMP以及它们的PRR被相继发现,这也将进一步助力于我们对植物与病原微生物共进化的认知,为未来植物病害防治奠定基础。

3 PRRs与卵菌的识别

大多数的卵菌是存在于土壤或水生环境的一类腐菌,可导致植物茎叶和块茎的毁灭性死亡,如马铃薯晚疫病病菌和葡萄霜霉病菌等。同样卵菌细胞壁的主要成分 β -1,3和 β -1,6葡聚糖、葡聚糖-壳聚糖、纤维素结合激酶凝集素,以及卵菌的转谷氨酰胺酶(Pep-13)、二十碳六烯酸和木葡聚糖特异性内切酶XEG1等均被认为是触发下游免疫响应的MAMP,但目前识别这些MAMP的PRR还未被证实(Raaymakers和Van den Ackerveken 2016)。在卵菌、真菌和细菌中还广泛存在这一类含有坏死的保守氨基酸肽和乙烯诱导肽样蛋白(NLPs),其含有20到24个相对保守的氨基酸位点,如nlp20和nlp24 (Bohm等2014; Oome等2014)。有研究显示在十字花科植物拟南芥中,LRR-RLP、RLP23可识别nlp20,并与SOBIR1和BAK1形成受体复合体共同激活植物防御反应(Albert等2015)。而对于茄科植物番茄来说,nlp20处理并不触发典型的植物细胞坏死,同时在番茄中异源表达拟南芥的RLP23又可增强植物对病原菌的抗性,再次说明不同植物种系在进化中对相同的MAMP可能形成了不同的识别机制(Bohm等2014)。

4 PRRs与DAMP的识别

为了更加高效地实现植物的免疫防御反应,植物除了可以感知外源MAMP的刺激,还可以感知由生物或非生物胁迫刺激后其自身产生的DAMP,从而进一步增强MAMP触发的免疫反应(Gust等2017)。在拟南芥中,蛋白多肽Peps就是一类可被膜受体蛋白PEPR1 (PLANT ELICITOR PEPTIDE RECEPTOR 1)和PEPR2 (PLANT ELICITOR PEPTIDE RECEPTOR 2)感知的DAMP (Krol等2010; Yamaguchi等2006, 2010)。PEPR1和Pep1的蛋白晶体结构显示,PEPR1识别Pep1的模式和FLS2识别

flg22的模式极其相似,且同样需要招募共受体BAK1激活下游信号(Tang等2015)。目前发现拟南芥中存在8种不同的Pep (Pep1~Pep8)多肽,均位于Pep前体蛋白PROPEP的C末端(Krol等2010; Yamaguchi等2006, 2010),且Peps之间存在高度的功能冗余,而它们前体蛋白的功能却存着潜在的差异,说明PROPEP除了参与植物免疫的调控可能还有其他新的功能(Bartels等2013)。虽然有研究发现植物在MAMP刺激后可诱导某些特定PROPEPs基因水平的上调表达,但PROPEPs是否在植物免疫反应触发前就已经被加工修饰,以及植物受到外源有害刺激后Peps如何分泌到细胞外间隙,当前还一无所知(Tintor等2013)。

寡聚半乳糖醛酸(oligogalacturonides, OGs)也是一种DAMP信号分子,是植物受到真菌或昆虫撕咬后,由植物细胞壁中多聚半乳糖醛酸降解而来,其可被与细胞壁紧密相连的受体WAK (CELL WALL-ASSOCIATED KINASE 1)和WAKL (WAK-like)识别,然后触发下游免疫信号(Bergey等1999; Brutus等2010; Denoux等2008; Ferrari等2013)。有研究发现PEPRs也参与了OG的感知和下游信号的激活(Gravino等2017),说明PEPRs可能和WAK或WAKL还存在着一些目前所不为人知的联系。

现在研究认为高迁移率族蛋白(high-mobility group box protein, HMGB)、胞外ATP (extracellular ATP, eATP)、角质、纤维二糖、PIPs (pattern-induced peptides) 和 RALF17 (RAPID ALKALINIZATION FACTORS 17)也是DAMP信号分子,但其研究相对较为浅薄,只发现L型凝集素类受体激酶DORN1 (DOES NOT RESPOND TO NUCLEOTIDES 1)参与eATP的感知(Chivasa等2009; Choi等2014), RLK7参与PIPs的感知(Hou等2014),以及Malectin类受体激酶参与RALF类多肽的感知(Stegmann等2017)。

5 PRRs介导的下游信号

当外源MAMP或内源DAMP被植物细胞膜上的PRRs识别后,即可触发植物第一层免疫防御反应—PTI,通过影响植物细胞内离子流的变化、MAPK信号途径的激活、活性氧的爆发而调控PTI早期信号,PTI后期反应则主要包括植物气孔的关

闭、胼胝质的沉积、植物激素的变化以及植保素的合成等,形成病原菌侵染植物的物理性屏障而抑制病原菌的侵害,从而进一步赋予植物一定程度的抗病能力(Yu等2017)。

当PTI信号被激活后,细胞内 Ca^{2+} 和 H^{+} 的内流以及 NO_3^- 、 K^{+} 和 Cl^- 的外流是植物PTI响应的早期反应之一(Jeworutzki等2010)。有研究显示,外源MAMP的短时间处理就可介导细胞内离子流的变化,进而迅速造成细胞膜去极化和细胞外碱化,但去极化的膜电位恢复至静息状态则需要相对较长的时间(Jeworutzki等2010; Pugin等1997)。细胞内 Ca^{2+} 的激增是植物PTI激活后的典型响应,且对于不同MAMP的刺激,细胞内 Ca^{2+} 在时间和空间上的浓度变化以及持续时间均有所不同,进而调控不同下游信号的响应,所以胞内 Ca^{2+} 的变化被认为是触发PTI下游信号的核心(Kwaaitaal等2011; Ranf等2011; Seybold等2014)。研究认为,细胞内 Ca^{2+} 浓度的迅速积累依赖于 Ca^{2+} 通道蛋白的被动运输以及 Ca^{2+} -ATPases和 Ca^{2+} 转运蛋白的主动运输,通过将细胞外空间和细胞器内部,如液泡和叶绿体中的 Ca^{2+} 迅速导入细胞质中而迅速升高胞内 Ca^{2+} 浓度(McAinsh和Pittman 2009; Dodd等2010)。目前研究发现, Ca^{2+} 通道蛋白CNGC2、CNGC4和OsCNGC9分别参与拟南芥和水稻中MAMP触发的 Ca^{2+} 内流(Ali等2007; Tian等2019; Wang等2019; Qi等2010)。最近有研究显示CNGC19也参与拟南芥的先天免疫反应,而且还与水稻的生长促进信号相关(Jogawat等2020)。另一类 Ca^{2+} 通道蛋白OSCA1.3则参与调控拟南芥的气孔免疫(Thor等2020)。这些通道蛋白在植物感知MAMP刺激后受到BIK1的磷酸化修饰,通过激活下游信号元件赋予植物相应的抗性免疫(Tian等2019, Thor等2020)。同时, Ca^{2+} 转运蛋白ACA4、ACA8、ACA10、ACA11、ACA12和ACA13也参与PTI介导的胞内 Ca^{2+} 内流(Frey等2012; Hilleary等2020; Yu等2018)。但是哪些元件调控 Ca^{2+} 转运蛋白的活性,以及受体复合体是否可以直接调控 Ca^{2+} 通道蛋白或转运蛋白的活性,目前还一无所知。

MAPK信号途径的激活同样也是PTI响应的早期反应。通过MAPK信号途径中一系列顺序磷酸

化, 将受体复合体的磷酸化信号往下传递至特定底物蛋白, 从而调控抗性基因的表达。目前研究认为, 拟南芥中MEKK3/MEKK5-MKK4/MKK5-MPK3/MPK6和MEKK1-MKK1/MKK2-MPK4两条信号途径参与PTI的响应, 同时磷酸化修饰的MPK3/MPK6和MPK4又可磷酸化修饰不同的下游底物调控植物的PTI响应(Asai等2002a; Kong等2012; Meng和Zhang 2013; Sun等2018)。

活性氧(reactive oxygen species, ROS)的爆发也是PTI响应的一个重要标志, 其产生依赖于细胞膜上的NADPH氧化酶RBOHD和过氧化物酶PRX33和PRX34的参与(Bindschedler等2006; Daudi等2012; Nühse等2007; Torres等2006)。在PTI信号中, RBOHD的激活既可以依赖于Ca²⁺, 通过Ca²⁺依赖蛋白激酶, 如CPK5、CPK6、CPK11和CPK4的磷酸化修饰而激活介导ROS的爆发; 又可以不依赖于Ca²⁺, 通过BIK1的磷酸化修饰而促进胞内ROS的大量积累(Boudsocq等2010; Dubiella等2013; Kadota等2014; Li等2014; Ogasawara等2008)。PRX-33和PRX34则直接受细胞分裂素受体ARR2的调控, 促进水杨酸或MAMP介导的ROS爆发(Arnaud等2017)。所以Ca²⁺、BIK1和ROS形成一个正反馈调节, 增强植物PTI响应。当然ROS的爆发也必然受到一些蛋白的负调控, 如CPK28通过磷酸化BIK1导致BIK1的降解, 和PBL13通过与RBOHD的互动而负调控ROS的产生, 从而最终维持细胞内ROS的稳态(Lin等2015; Monaghan等2014)。

6 总结与展望

从第一个植物免疫受体发现至今, 我们虽然对植物免疫信号通路的调控有些初步了解, 但仍然有很多的PRRs、MAMPs或DAMPs可能并未被发现(表1)。同时, 不同PRR调控的下游信号通路是否共用, 以及植物对不同MAMPs或DAMPs触发的PTI响应是否存在程度上的差异等科学问题均有待进一步的研究发现。从进化的角度来看, 植物和病原微生物在进化过程中相互牵制, 此消彼长, 所以基于植物和病原微生物的遗传信息, 并结合进化分析可能有助于我们进一步发现新的免疫受体和相应的MAMPs。从信号转导的角度来看,

表1 植物模式识别受体与配体			
Table 1 Plant pattern recognition receptors and their ligands			
模式识别受体	类型	配体	受体来源
识别真菌的受体			
CERK1	LysM-RLK	Chitin	拟南芥
LYK4/5	LysM-RLK	Chitin	拟南芥
CEBiP	LysM-RLP	Chitin	水稻
Eix1/2	LRR-RLP	EIX	番茄
RLP42/RBGP1	LRR-RLP	PGs	拟南芥
识别细菌的受体			
FLS2	LRR-RLK	flg22	拟南芥
FLS2	LRR-RLK	flg15	番茄
FLS3	LRR-RLK	flgII-28	番茄
EFR	LRR-RLK	elf18	拟南芥
LYM1/3	LysM-RLP	PGNs	拟南芥
LYP4/6	LysM-RLP	PGNs	水稻
LORE/SD1-29	LEC-RLK	LPS	拟南芥
识别卵菌的受体			
RLP23	LRR-RLP	nlp20/40	拟南芥
识别DAMP的受体			
PEPRs	LRR-RLK	Peps	拟南芥
WAK/WAKL	EGF-like-RLK	OGs	拟南芥
RLK7	LRR-RLK	PIPs	拟南芥
FER	Malectin-RLK	RALFs	拟南芥

RLK: receptor-like protein kinase; RLP: receptor-like protein; LRR: leucine-rich repeat; LysM: lysin motif; LEC: lectin; EGF: epidermal growth factor. EIX: Ethylene-inducing xylanase; PGs: Endopolygalacturonases; PGNs: Peptidoglycans; LPS: Lipopolysaccharide; OGs: Oligogalacturonides.

BAK1作为多个不同PRR的共受体参与调控植物的先天免疫响应, 无疑是PTI信号途径中的核心元件, 可能起到整合多条免疫信号通路的作用, 使植物在受到不同MAMPs或DAMPs刺激时产生相似的下流响应(图2)。但对于病原菌而言, 其直接攻击BAK1很容易造成多条PTI信号途径的中断, 貌似对植物来说并不是最佳的进化选择。而植物在漫长的进化中仍然将BAK1做为PTI信号通路中的核心组分, 暗示着BAK1在调控PTI信号通路外还可能存在着其他未知的功能和作用。所以植物的PTI信号网络看似简单, 其实可能错综复杂, 各个信号直接或间接相互协调, 共同调节植物的免疫

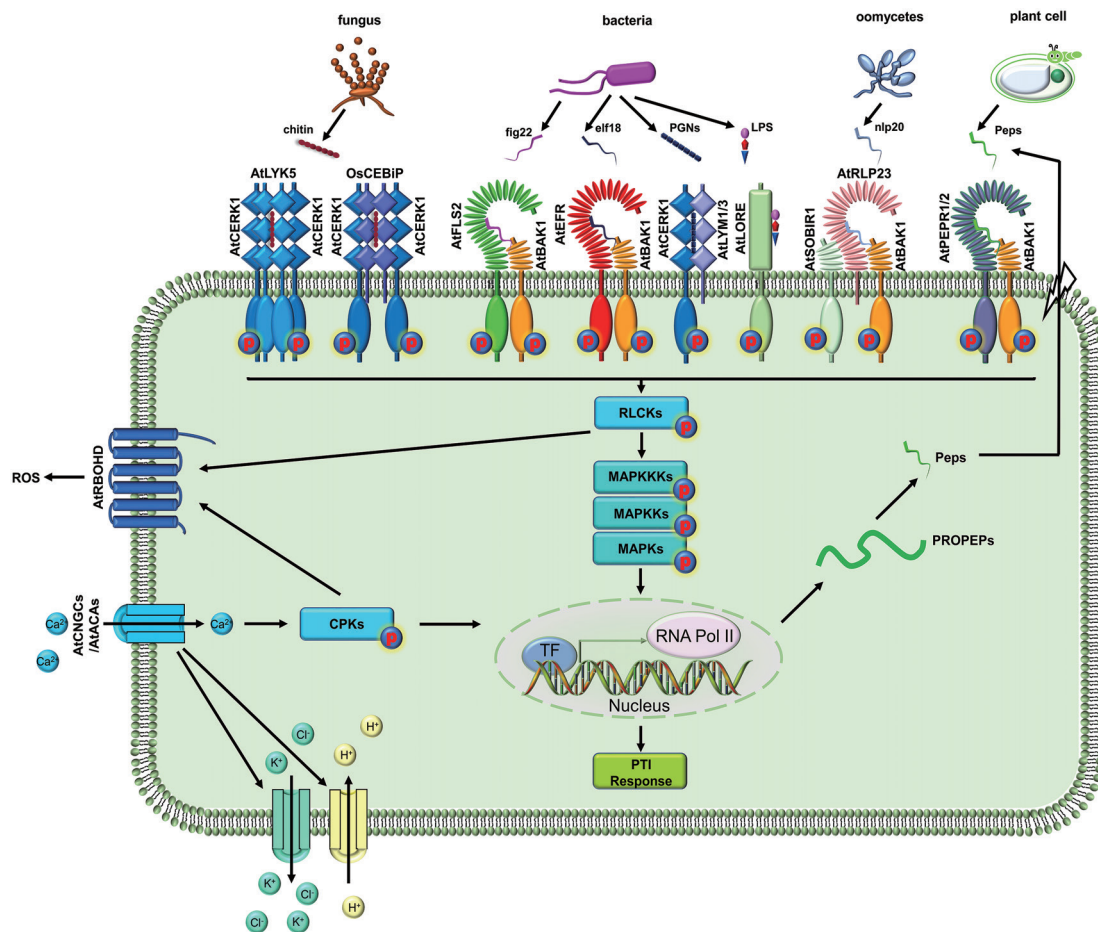


图2 植物模式识别受体与先天免疫

Fig. 2 Plant pattern recognition receptors and innate immunity

防御与生长发育, 因此对PTI信号通路中各成员的深入了解将有助于深入理解植物与病原微生物协同进化的机制, 对培育抗病作物, 发展绿色农业, 助力脱贫攻坚, 解决食品安全问题均具有现实意义。

参考文献(References)

- Albert I, Böhm H, Albert M, et al (2015). An RLP23-SO-BIR1-BAK1 complex mediates NLP-triggered immunity. *Nat Plants*, 1: 15140
- Ali R, Ma W, Lemtiri-Chlieh F, et al (2007). Death don't have no mercy and neither does calcium: *Arabidopsis* CYCLIC NUCLEOTIDE GATED CHANNEL2 and innate immunity. *Plant Cell*, 19: 1081–1095
- Arnaud D, Lee S, Takebayashi Y, et al (2017). Cytokinin-mediated regulation of reactive oxygen species homeostasis modulates stomatal immunity in *Arabidopsis*. *Plant Cell*, 29: 543–559
- Bar M, Sharfman M, Ron M, et al (2010). BAK1 is required for the attenuation of ethylene-inducing xylanase (Eix)-induced defense responses by the decoy receptor LeEix1. *Plant J*, 63: 791–800
- Bartels S, Lori M, Mbengue M, et al (2013). The family of Peps and their precursors in *Arabidopsis*: differential expression and localization but similar induction of pattern-triggered immune responses. *J Exp Bot*, 64: 5309–5321
- Bauer Z, Gómez-Gómez L, Boller T, et al (2001). Sensitivity of different ecotypes and mutants of *Arabidopsis thaliana* toward the bacterial elicitor flagellin correlates with the presence of receptor-binding sites. *J Biol Chem*, 276: 45669–45676
- Bergey DR, Orozco-Cardenas M, de Moura DS, et al (1999). A wound- and systemin-inducible polygalacturonase in tomato leaves. *Proc Natl Acad Sci USA*, 96: 1756–1760
- Bindschedler LV, Dewdney J, Blee KA et al (2006). Peroxi-

- dase-dependent apoplastic oxidative burst in *Arabidopsis* required for pathogen resistance. *Plant J*, 47: 851–863
- Böhm H, Albert I, Oome S, et al (2014). A conserved peptide pattern from a widespread microbial virulence factor triggers pattern-induced immunity in *Arabidopsis*. *PLOS Pathog*, 10: e1004491
- Boller T, Felix G (2009). A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. *Annu Rev Plant Biol*, 60: 379–406
- Boudsocq M, Willmann MR, McCormack M, et al (2010). Differential innate immune signalling via Ca^{2+} sensor protein kinases. *Nature*, 464: 418–422
- Bozsoki Z, Gysel K, Hansen SB, et al (2020). Ligand-recognizing motifs in plant LysM receptors are major determinants of specificity. *Science*, 369: 663–670
- Broghammer A, Krusell L, Blaise M, et al (2012). Legume receptors perceive the rhizobial lipochitin oligosaccharide signal molecules by direct binding. *Proc Natl Acad Sci USA*, 109: 13859–13864
- Brutus A, Sicilia F, Macone A, et al (2010). A domain swap approach reveals a role of the plant wall-associated kinase 1 (WAK1) as a receptor of oligogalacturonides. *Proc Natl Acad Sci USA*, 107: 9452–9457
- Buscaill P, Chandrasekar B, Sanguankiatichai N, et al (2019). Glycosidase and glycan polymorphism control hydrolytic release of immunogenic flagellin peptides. *Science*, 364: eaav0748
- Cao YR, Liang Y, Tanaka K, et al (2014). The kinase LYK5 is a major chitin receptor in *Arabidopsis* and forms a chitin-induced complex with related kinase CERK1. *Elife*, 3: e03766
- Chinchilla D, Bauer Z, Regenass M, et al (2006). The *Arabidopsis* receptor kinase FLS2 binds flg22 and determines the specificity of flagellin perception. *Plant Cell*, 18: 465–476
- Chinchilla D, Boller T, Robatzek S (2007). Flagellin signalling in plant immunity. *Adv Exp Med Biol*, 598: 358–371
- Chivasa S, Murphy AM, Hamilton JM, et al (2009). Extracellular ATP is a regulator of pathogen defence in plants. *Plant J*, 60: 436–448
- Choi J, Tanaka K, Cao YR, et al (2014). Identification of a plant receptor for extracellular ATP. *Science*, 343: 290–294
- Collinge DB, Kragh KM, Mikkelsen JD, et al (1993). Plant chitinases. *Plant J*, 3: 31–40
- Cook DE, Mesarich CH, Thomma BPHJ (2015). Understanding plant immunity as a surveillance system to detect invasion. *Annu Rev Phytopathol*, 53: 541–563
- Danna CH, Millet YA, Koller T, et al (2011). The *Arabidopsis* flagellin receptor FLS2 mediates the perception of *Xanthomonas* Ax21 secreted peptides. *Proc Natl Acad Sci USA*, 108: 9286–9291
- Daudi A, Cheng ZY, O'Brien JA, et al (2012). The apoplastic oxidative burst peroxidase in *Arabidopsis* is a major component of pattern-triggered immunity. *Plant Cell*, 24: 275–287
- Deller S, Hammond-Kosack KE, Rudd JJ (2011). The complex interactions between host immunity and non-biotrophic fungal pathogens of wheat leaves. *J Plant Physiol*, 168: 63–71
- Denoux C, Galletti R, Mammarella N, et al (2008). Activation of defense response pathways by OGs and Flg22 elicitors in *Arabidopsis* seedlings. *Mol Plant*, 1: 423–445
- Dodd AN, Kudla J, Sanders D (2010). The language of calcium signaling. *Annu Rev Plant Biol*, 61: 593–620
- Dubiella U, Seybold H, Durian G, et al (2013). Calcium-dependent protein kinase/NADPH oxidase activation circuit is required for rapid defense signal propagation. *Proc Natl Acad Sci USA*, 110: 8744–8749
- Feng F, Sun J, Radhakrishnan GV, et al (2019). A combination of chitooligosaccharide and lipochitooligosaccharide recognition promotes arbuscular mycorrhizal associations in *Medicago truncatula*. *Nat Commun*, 10: 5047
- Ferrari S, Savatin DV, Sicilia F, et al (2013). Oligogalacturonides: plant damage-associated molecular patterns and regulators of growth and development. *Front Plant Sci*, 4: 49
- Frey NFD, Mbengue M, Kwaaitaal M, et al (2012). Plasma membrane calcium ATPases are important components of receptor-mediated signaling in plant immune responses and development. *Plant Physiol*, 159: 798–809
- Gómez-Gómez L, Bauer Z, Boller T (2001). Both the extracellular leucine-rich repeat domain and the kinase activity of FLS2 are required for flagellin binding and signaling in *Arabidopsis*. *Plant Cell*, 13: 1155–1163
- Gravino M, Locci F, Tundo S, et al (2017). Immune responses induced by oligogalacturonides are differentially affected by AvrPto and loss of BAK1/BKK1 and PEPR1/PEPR2. *Mol Plant Pathol*, 18: 582–595
- Gust AA, Pruitt R, Nürnberger T (2017). Sensing danger: key to activating plant immunity. *Trends Plant Sci*, 22: 779–791
- Han LB, Li YB, Wang FX, et al (2019). The cotton apoplastic protein CRR1 stabilizes chitinase 28 to facilitate defense against the fungal pathogen *Verticillium dahliae*. *Plant Cell*, 31: 520–536
- Hilleary R, Paez-Valencia J, Vens C, et al (2020). Tonoplast-localized Ca^{2+} pumps regulate Ca^{2+} signals during pattern-triggered immunity in *Arabidopsis thaliana*. *Proc*

- Natl Acad Sci USA, 17: 18849–18857
- Hind SR, Strickler SR, Boyle PC, et al (2016). Tomato receptor FLAGELLIN-SENSING 3 binds flgII-28 and activates the plant immune system. *Nat Plants*, 2: 16128
- Hou SG, Wang X, Chen DH, et al (2014). The secreted peptide PIP1 amplifies immunity through Receptor-Like Kinase 7. *PLOS Pathog*, 10: e1004331
- Iizasa E, Mitsutomi M, Nagano Y (2010). Direct binding of a plant LysM receptor-like kinase, LysM RLK1/CERK1, to chitin *in vitro*. *J Biol Chem*, 285: 2996–3004
- Jeworutzki E, Roelfsema MR, Anschutz U, et al (2010). Early signaling through the *Arabidopsis* pattern recognition receptors FLS2 and EFR involves Ca-associated opening of plasma membrane anion channels. *Plant J*, 62: 367–378
- Jogawat A, Meena MK, Kundu A, et al (2020). Calcium channel CNGC19 mediates basal defense signaling to regulate colonization by *Piriformospora indica* in *Arabidopsis* roots. *J Exp Bot*, 71: 2752–2768
- Jones JD, Dangl JL (2006). The plant immune system. *Nature*, 444: 323–329
- Jose J, Ghantasala S, Roy Choudhury S (2020). *Arabidopsis* transmembrane receptor-like kinases (RLKs): a bridge between extracellular signal and intracellular regulatory machinery. *Int J Mol Sci*, 21: 4000
- Kadota Y, Sklenar J, Derbyshire P, et al (2014). Direct regulation of the NADPH oxidase RBOHD by the PRR-associated kinase BIK1 during plant immunity. *Mol Cell*, 54: 43–55
- Kagan JC (2017). Lipopolysaccharide detection across the kingdoms of life. *Trends Immunol*, 38: 696–704
- Kaku H, Nishizawa Y, Ishii-Minami N, et al (2006). Plant cells recognize chitin fragments for defense signaling through a plasma membrane receptor. *Proc Natl Acad Sci USA*, 103: 11086–11091
- Katagiri F, Tsuda K (2010). Understanding the plant immune system. *Mol Plant Microbe Interact*, 23: 1531–1536
- Kawaharada Y, Kelly S, Nielsen MW, et al (2015). Receptor-mediated exopolysaccharide perception controls bacterial infection. *Nature*, 523: 308–312
- Kombrink A, Sánchez-Vallet A, Thomma BPHJ (2011). The role of chitin detection in plant-pathogen interactions. *Microbes Infect*, 13: 1168–1176
- Krol E, Mentzel T, Chinchilla D, et al (2010). Perception of the *Arabidopsis* danger signal peptide 1 involves the pattern recognition receptor AtPEPR1 and its close homologue AtPEPR2. *J Biol Chem*, 285: 13471–13479
- Kunze G, Zipfel C, Robatzek S, et al (2004). The N terminus of bacterial elongation factor Tu elicits innate immunity in *Arabidopsis* plants. *Plant Cell*, 16: 3496–3507
- Kwaaitaal M, Huisman R, Maintz J, et al (2011). Ionotropic glutamate receptor (iGluR)-like channels mediate MAMP-induced calcium influx in *Arabidopsis thaliana*. *Biochem J*, 440: 355–365
- Lacombe S, Rougon-Cardoso A, Sherwood E, et al (2010). Interfamily transfer of a plant pattern-recognition receptor confers broad-spectrum bacterial resistance. *Nat Biotechnol*, 28: 365–369
- Li L, Li M, Yu LP, et al (2014). The FLS2-associated kinase BIK1 directly phosphorylates the NADPH oxidase RbohD to control plant immunity. *Cell Host Microbe*, 15: 329–338
- Lin ZJD, Liebrand TWH, Yadeta KA, et al (2015). PBL13 is a serine/threonine protein kinase that negatively regulates *Arabidopsis* immune responses. *Plant Physiol*, 169: 2950–2962
- Liu B, Li JF, Ao Y, et al (2012a). Lysin motif-containing proteins LYP4 and LYP6 play dual roles in peptidoglycan and chitin perception in rice innate immunity. *Plant Cell*, 24: 3406–3419
- Liu SM, Wang JZ, Han ZF, et al (2016). Molecular mechanism for fungal cell wall recognition by rice chitin receptor OsCEBiP. *Structure*, 24: 1192–1200
- Liu TT, Liu ZX, Song CJ, et al (2012b). Chitin-induced dimerization activates a plant immune receptor. *Science*, 336: 1160–1164
- Liu XK, Grabherr HM, Willmann R, et al (2014). Host-induced bacterial cell wall decomposition mediates pattern-triggered immunity in *Arabidopsis*. *Elife*, 3: e01990
- Macho AP, Zipfel C (2014). Plant PRRs and the activation of innate immune signaling. *Mol Cell*, 54: 263–272
- Madsen EB, Madsen LH, Radutoiu S, et al (2003). A receptor kinase gene of the LysM type is involved in legume perception of rhizobial signals. *Nature*, 425: 637–640
- McAinsh MR, Pittman JK (2009). Shaping the calcium signature. *New Phytol*, 181: 275–294
- Meindl T, Boller T, Felix G (2000). The bacterial elicitor flagellin activates its receptor in tomato cells according to the address-message concept. *Plant Cell*, 12: 1783–1794
- Miya A, Albert P, Shinya T, et al (2007). CERK1, a LysM receptor kinase, is essential for chitin elicitor signaling in *Arabidopsis*. *Proc Natl Acad Sci USA*, 104: 19613–19618
- Monaghan J, Matschi S, Shorinola O, et al (2014). The calcium-dependent protein kinase CPK28 buffers plant immunity and regulates BIK1 turnover. *Cell Host Micro*, 16: 605–615
- Nühse TS, Bottrill AR, Jones AME, et al (2007). Quantitative phosphoproteomic analysis of plasma membrane proteins reveals regulatory mechanisms of plant innate immune responses. *Plant J*, 51: 931–940
- Ogasawara Y, Kaya H, Hiraoka G, et al (2008). Synergistic ac-

- tivation of the *Arabidopsis* NADPH oxidase AtrbohD by Ca^{2+} and phosphorylation. *J Biol Chem*, 283: 8885–8892
- Oome S, Raaymakers TM, Cabral A, et al (2014). Nep1-like proteins from three kingdoms of life act as a microbe-associated molecular pattern in *Arabidopsis*. *Proc Natl Acad Sci USA*, 111: 16955–16960
- Petutschnig EK, Jones AME, Serazetdinova L, et al (2010). The Lysin motif receptor-like kinase (LysM-RLK) CERK1 is a major chitin-binding protein in *Arabidopsis thaliana* and subject to chitin-induced phosphorylation. *J Biol Chem*, 285: 28902–28911
- Poinssot B, Vandelle E, Bentéjac M, et al (2003). The endopolygalacturonase 1 from *Botrytis cinerea* activates grapevine defense reactions unrelated to its enzymatic activity. *Mol Plant Microbe Interact*, 16: 553–564
- Pugin A, Frachisse JM, Tavernier E, et al (1997). Early events induced by the elicitor cryptogin in tobacco cells: involvement of a plasma membrane NADPH oxidase and activation of glycolysis and the pentose phosphate pathway. *Plant Cell*, 9: 2077–2091
- Qi Z, Verma R, Gehring C, et al (2010). Ca^{2+} signaling by plant *Arabidopsis thaliana* Pep peptides depends on AtPepR1, a receptor with guanylyl cyclase activity, and cGMP-activated Ca^{2+} channels. *Proc Natl Acad Sci USA*, 107: 21193–21198
- Raaymakers TM, Van den Ackerveken G (2016). Extracellular Recognition of Oomycetes during Biotrophic Infection of Plants. *Front Plant Sci*, 7: 906
- Ranf S (2016). Immune sensing of lipopolysaccharide in plants and animals: same but different. *PLOS Pathog*, 12: e1005596
- Ranf S, Eschen-Lippold L, Pecher P, et al (2011). Interplay between calcium signalling and early signalling elements during defence responses to microbe- or damage-associated molecular patterns. *Plant J*, 68: 100–113
- Ranf S, Gisch N, Schäffer M, et al (2015). A lectin S-domain receptor kinase mediates lipopolysaccharide sensing in *Arabidopsis thaliana*. *Nat Immunol*, 16: 426–433
- Robatzek S, Bittel P, Chinchilla D, et al (2007). Molecular identification and characterization of the tomato flagellin receptor LeFLS2, an orthologue of *Arabidopsis* FLS2 exhibiting characteristically different perception specificities. *Plant Mol Biol*, 64: 539–547
- Ron M, Avni A (2004). The receptor for the fungal elicitor ethylene-inducing xylanase is a member of a resistance-like gene family in tomato. *Plant Cell*, 16: 1604–1615
- Savary S, Willocquet L, Pethybridge SJ, et al (2019). The global burden of pathogens and pests on major food crops. *Nat Ecol Evol*, 3: 430–439
- Seybold H, Trempel F, Ranf S, et al (2014). Ca^{2+} signalling in plant immune response: from pattern recognition receptors to Ca^{2+} decoding mechanisms. *New Phytol*, 204: 782–790
- Shimizu T, Nakano T, Takamizawa D, et al (2010). Two LysM receptor molecules, CEBiP and OsCERK1, cooperatively regulate chitin elicitor signaling in rice. *Plant J*, 64: 204–214
- Shiu SH, Bleecker AB (2001). Plant receptor-like kinase gene family: diversity, function, and signaling. *Sci STKE*, 2001: re22
- Stegmann M, Monaghan J, Smakowska-Luzan E, et al (2017). The receptor kinase FER is a RALF-regulated scaffold controlling plant immune signaling. *Science*, 355: 287–289
- Sun YD, Li L, Macho AP, et al (2013). Structural basis for flg22-induced activation of the *Arabidopsis* FLS2-BAK1 immune complex. *Science*, 342: 624–628
- Sun TJ, Nitta Y, Zhang Q, et al (2018). Antagonistic interactions between two MAP kinase cascades in plant development and immune signaling. *Embo Rep*, 19: e45324
- Takai R, Isogai A, Takayama S, et al (2008). Analysis of flagellin perception mediated by flg22 receptor OsFLS2 in rice. *Mol Plant Microbe Interact*, 21: 1635–1642
- Tang J, Han ZF, Sun YD, et al (2015). Structural basis for recognition of an endogenous peptide by the plant receptor kinase PEPR1. *Cell Res*, 25: 110–120
- Thor K, Jiang SS, Michard E, et al (2020). The calcium-permeable channel OSCA1.3 regulates plant stomatal immunity. *Nature*, 585: 569–573
- Tian W, Hou CC, Ren ZJ, et al (2019). A calmodulin-gated calcium channel links pathogen patterns to plant immunity. *Nature*, 572: 131–135
- Tintor N, Ross A, Kanehara K, et al (2013). Layered pattern receptor signaling via ethylene and endogenous elicitor peptides during *Arabidopsis* immunity to bacterial infection. *Proc Natl Acad Sci USA*, 110: 6211–6216
- Torres MA, Jones JDG, Dangl JL (2006). Reactive oxygen species signaling in response to pathogens. *Plant Physiol*, 141: 373–378
- Wan JR, Tanaka K, Zhang XC, et al (2012). LYK4, a lysin motif receptor-like kinase, is important for chitin signaling and plant innate immunity in *Arabidopsis*. *Plant Physiol*, 160: 396–406
- Wan JR, Zhang XC, Neece D, et al (2008). A LysM receptor-like kinase plays a critical role in chitin signaling and fungal resistance in *Arabidopsis*. *Plant Cell*, 20: 471–481
- Wang JC, Liu X, Zhang A, et al (2019). A cyclic nucleotide-gated channel mediates cytoplasmic calcium elevation and disease resistance in rice. *Cell Res*, 29: 820–831
- Wang GD, Ellendorff U, Kemp B, et al (2008). A ge-

- nome-wide functional investigation into the roles of receptor-like proteins in *Arabidopsis*. *Plant Physiol*, 147: 503–517
- Wang SZ, Sun Z, Wang HQ, et al (2015). Rice OsFLS2-mediated perception of bacterial flagellins is evaded by *Xanthomonas oryzae* pvs. *oryzae* and *oryzicola*. *Mol Plant*, 8: 1024–1037
- Willmann R, Lajunen HM, Erbs G, et al (2011). *Arabidopsis* lysin-motif proteins LYM1 LYM3 CERK1 mediate bacterial peptidoglycan sensing and immunity to bacterial infection. *Proc Natl Acad Sci USA*, 108: 19824–19829
- Wu Y, Zhou JM (2013). Receptor-like kinases in plant innate immunity. *J Integr Plant Biol*, 55: 1271–1286
- Yamaguchi Y, Huffaker A, Bryan AC, et al (2010). PEPR2 is a second receptor for the Pep1 and Pep2 peptides and contributes to defense responses in *Arabidopsis*. *Plant Cell*, 22: 508–522
- Yamaguchi Y, Pearce G, Ryan CA (2006). The cell surface leucine-rich repeat receptor for AtPep1, an endogenous peptide elicitor in *Arabidopsis*, is functional in transgenic tobacco cells. *Proc Natl Acad Sci USA*, 103: 10104–10109
- Yamamoto M, Ohnishi-Kameyama M, Nguyen CL, et al (2011). Identification of genes involved in the glycosylation of modified viosamine of flagellins in *Pseudomonas syringae* by mass spectrometry. *Genes*, 2: 788–803
- Ye WX, Munemasa S, Shinya T, et al (2020). Stomatal immunity against fungal invasion comprises not only chitin-induced stomatal closure but also chitosan-induced guard cell death. *Proc Natl Acad Sci USA*, 117: 20932–20942
- Yu HY, Yan JP, Du XG, et al (2018). Overlapping and differential roles of plasma membrane calcium ATPases in *Arabidopsis* growth and environmental responses. *J Exp Bot*, 69: 2693–2703
- Yu X, Feng BM, He P, et al (2017). From chaos to harmony: responses and signaling upon microbial pattern recognition. *Annu Rev Phytopathol*, 55: 109–137
- Zhang LS, Kars I, Essenstam B, et al (2014). Fungal endopolygalacturonases are recognized as microbe-associated molecular patterns by the *Arabidopsis* receptor-like protein RESPONSIVENESS TO BOTRYTIS POLYGALACTURONASES1. *Plant Physiol*, 164: 352–364
- Zhang XC, Cannon SB, Stacey G (2009). Evolutionary genomics of *LysM* genes in land plants. *BMC Evol Biol*, 9: 183
- Zipfel C, Kunze G, Chinchilla D, et al (2006). Perception of the bacterial PAMP EF-Tu by the receptor EFR restricts *Agrobacterium*-mediated transformation. *Cell*, 125: 749–760