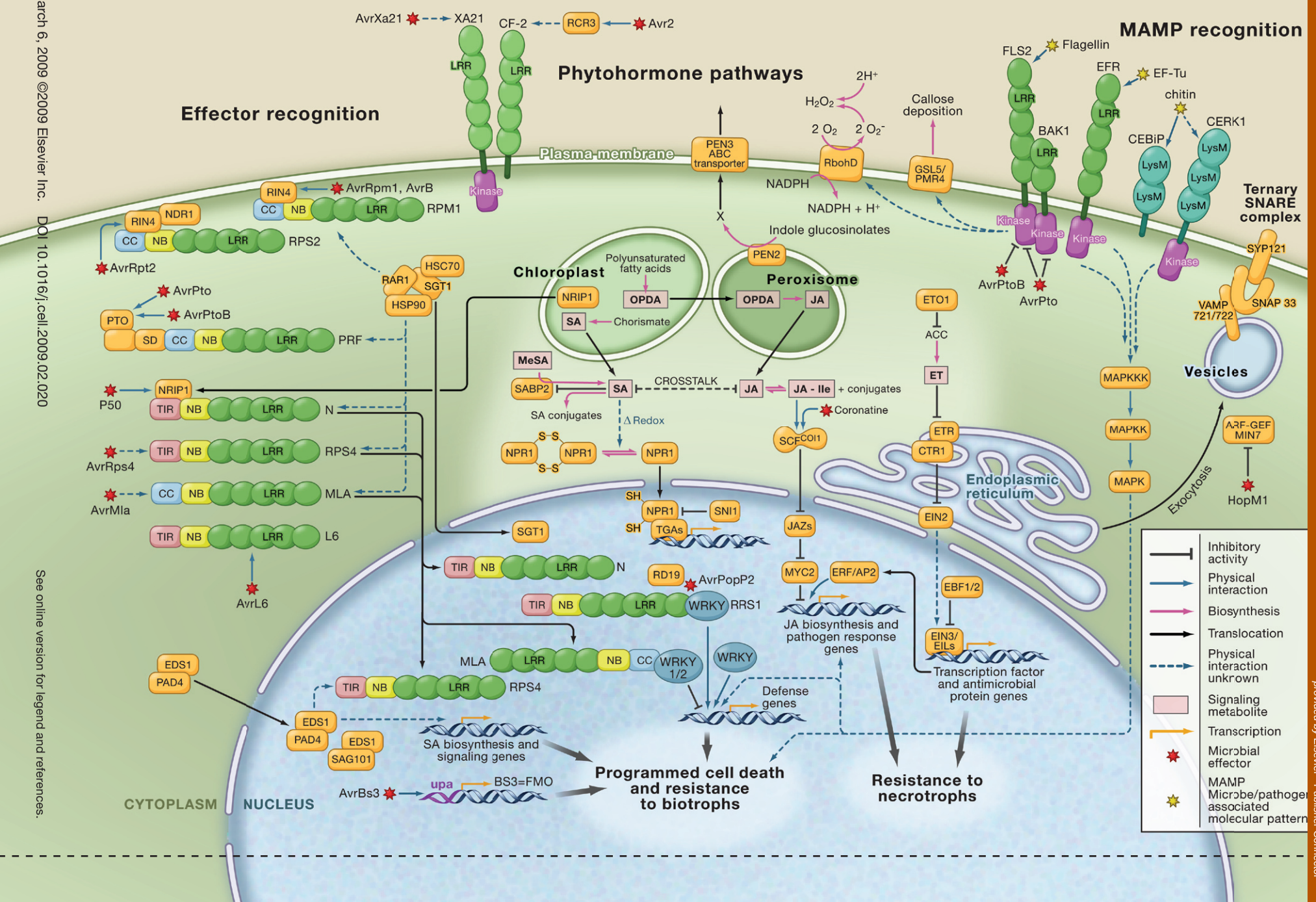
SnapShot: Plant Immune Response Pathways

Ralph Panstruga, Jane E. Parker, and Paul Schulze-Lefert
Max-Planck Institute for Plant Breeding Research, Köln 50829, Germany

Cell



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Recognition of Microbe/Pathogen-Associated Molecular Patterns

Plant innate immunity depends on the timely discrimination of self from nonself, which, as in animal cells, can be accomplished by membrane-anchored pattern recognition receptors (PRRs). These receptors monitor the exterior space for microbe/pathogen-associated molecular patterns or MAMPs (also called PAMPs) by binding to them directly or by associating with MAMP-binding proteins. Well-characterized plant PRRs comprise leucine-rich repeat (LRR) receptor-like kinases such as the flagellin receptor FLS2, its coreceptor BAK1, and the receptor for bacterial elongation factor EF-Tu called EFR. Membrane-bound proteins with peptidoglycan-binding LysM domains (for example, CEBiP and CERK1) represent PRRs or binding proteins for the fungal MAMP, chitin. Recognition of conserved MAMPs by PRRs triggers intracellular signaling via mitogen-activated protein kinase (MAPK) cascades (MAPKKK, MAPKK, MAPK). This results ultimately in transcriptional activation of defense genes by plant-specific transcriptional regulators including members of the WRKY superfamily. Execution of the immune response relies in part on the exocytosis pathway leading to vesicle-associated and SNARE protein-mediated focal secretion of defense-related proteins including PR-1. A "toxic load" of antimicrobial cargo such as that derived from the biochemical activation of nontoxic precursors can also be translocated to the extracellular space by members of the ATP-binding cassette (ABC) transporter family. Another early MAMP-triggered response is the extracellular generation of reactive oxygen species (O_2^- and H_2O_2) by membrane-localized NADPH oxidases (RbohD). In contrast, biosynthesis and deposition of the polyglucan callose (by the GSL5/PMR4 callose synthase) in the extracellular space is a comparatively late defense-associated response. Microbial effector proteins (such as AvrPto, AvrPtoB, HopM1) intercept innate immune responses at the level of MAMP signaling or by targeting the secretory defense execution machinery. For example, HopM1 binds to the ARF-GEF, MIN7, of *Arabidopsis* leading to ubiquitination-dependent proteolysis of MIN7.

Effector Recognition

Plant resistance (R) proteins define an intracellular class of pattern recognition receptors (RPM1, RPS2, PRF, N, RPS4, MLA, L6) but also include a few sensors in the plasma membrane (CF-2, XA21). R proteins detect directly or indirectly isolate-specific pathogen effectors encoded by avirulence (*Avr*) genes such as AvrRpm1, AvrB, and AvrRpt2. Like PRR-triggered immune responses, R protein-conditioned immunity is linked to accumulation of reactive oxygen species and activation of defense genes but differs both quantitatively and kinetically from the former and typically leads to programmed host cell death at sites of attempted invasion. This "hypersensitive response" is thought to limit the spread of infection. Because PRR- and R protein-triggered output responses are similar, it is likely that their signaling pathways converge. A central nucleotide-binding (NB) domain and C-terminal LRRs are common structural modules found in plant R proteins. Most intracellular R proteins contain an N-terminal coiled coil (CC) or TOLL/Interleukin-1 receptor (TIR) domain. The NB domain is part of a larger domain called NB-ARC, which is found in plant R proteins, the APAF-1 (apoptotic regulators human apoptotic protease-activating factor 1) protein of mammals, and its *Caenorhabditis elegans* homolog CED-4. Proteins containing the NB-ARC domain belong to the family of STAND (signal transduction ATPases with numerous domains) NTPases and may act as regulatory signal transduction switches. Many R proteins require for their function the cytosolic chaperones HSP90 and HSC70 as well as the co-chaperones RAR1 and SGT1. This folding machinery is typically engaged in the synthesis of autorepressed receptors. Translocation of several intracellular R proteins into the nucleus is required for immune response activation, suggesting the operation of short signaling pathways leading to direct transcriptional reprogramming of host cells for immune response activation.

Phytohormone Pathways

A complex network of signaling pathways induced by phytohormones—such as salicylic acid (SA), gaseous ethylene (ET), and jasmonic acid (JA)—regulates local and systemic resistance to invasive pathogens. Crosstalk between different hormone systems allows the plant to respond appropriately to a particular mode of pathogen infection and to integrate biotic and abiotic stress stimuli. Accumulation of the phenolic hormone SA and SA derivatives is important for resistance to biotrophic pathogens that require living plant cells for reproduction. Activated intracellular TIR-NB-LRR receptors are particularly effective at stimulating SA biosynthesis and signaling through the nucleo-cytoplasmic regulators, EDS1 and PAD4. SA is sensed by the transcription cofactor NPR1, which, upon changes in cellular redox status (Δ Redox), becomes activated and moves into the nucleus where it modulates expression of antimicrobial and secretory pathway genes needed for systemic resistance. By contrast, the lipid-derived hormone JA and JA conjugates cooperate with ET to regulate resistance to necrotrophic pathogens that kill plant cells as they reproduce. JA conjugates stimulate SCF (Skp-Cullin-F-box) E3 ubiquitin ligase-mediated degradation of JAZ (jasmonate ZIM-domain) repressors of transcription factors such as MYC2. This leads to induced expression of genes for JA biosynthesis. ET is sensed by a family of ER-associated ET receptors (ETRs) that initiate a regulatory cascade leading ultimately to stabilization and activation of transcription factors, such as EIN3, and changes in gene expression. The JA and ET pathways are integrated at the level of the transcriptional machinery by closely coordinated induction of defense pathways. Antagonism between SA and JA/ET response systems occurs at multiple levels and has been exploited by some pathogens to promote disease (e.g., production of the JA-Ile mimic, coronatine, by *Pseudomonas syringae*). An emerging theme in plant stress hormone signaling is the hormone-induced activation of transcription factors by removal of negative regulators. Also, engagement of multiple positive and negative feedback loops allows rapid adjustment of plant cells to a prevailing stress stimulus or a return to the ground state.

Abbreviations

ACC, 1-aminocyclopropane-1-carboxylic acid; ARF-GEF, ADP ribosylation factor hydrolyzing guanidine triphosphate; FMO, flavin-containing monooxygenase; JA-Ile, jasmonoyl-isoleucine conjugate; MeSA, methyl salicylate; OPDA, oxophytodienoic acid; SD, solanaceae domain; SNARE, soluble *N*-ethylmalemide-sensitive factor attachment protein receptor; S-S and SH, oxidized disulphide and reduced sulfhydryl group; upa, *cis*-acting promoter element for AvrsBs3.

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